

# MEMOIRS

OF THE

# QUEENSLAND MUSEUM



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## PREFACE

### *HUMPBACK WHALE CONFERENCE 2000*

The Queensland Museum held its second international humpback whale conference in late August and early September 2000. Resultant papers and abstracts from the proceedings are contained in this issue of the *Memoirs of the Queensland Museum*. The contents reflect research diversity relating to this ubiquitous species which frequents coastal waters for substantial periods during its migration. A highlight of the conference was the opportunity, generously provided by Kerry López of Moreton Bay Whalewatching, to observe humpback whales close to the southern Queensland coast in the vicinity of the former whaling ground at Cape Moreton. For Queensland, the presence of humpback whales in these and other local waters is important both from an historical viewpoint and currently in tourism and research potential.

The conference presented an excellent opportunity for researchers to exchange ideas in a relaxed atmosphere. Delegates from Australia, New Zealand, North and South America, Oceania and South Africa availed themselves of this opportunity. Contributions of young researchers were an important feature of the conference and are reflected in this issue. Travel prizes to assist attendance by some of those researchers were awarded to Luciano Dalla Rosa and Eduardo Secchi (Brazil), Erin Falcone (USA) and Michael Noad (Australia).

Papers in this issue reflect concerns with, hopefully, the last period of exploitation which ended in the 1960s, as well as cautious optimism with regard to the future of this species which has become a conservation focus not only because of its former plight but also by its eerie songs and spectacular behaviour during its annual migration.

The Queensland Museum is proud to have hosted the conference and acknowledges the generous support of National Tour Company, Stradbroke Ferries and Tangalooma Island Resort. Kintetsu International, by means of an earlier donation to the Museum for the purpose of whale research, has considerably defrayed publication costs and a recent donation from Moreton Bay Whalewatching enabled colour printing in a number of papers.

The conference was convened by Robert Paterson and organised with much assistance from Patricia Paterson and Heather Janetzki. Success of the event was also due to Steve Van Dyck, Andrew Arney and Andrew Baker.

*Paul Avern, Brisbane, 31 December 2001.*

COVER: A humpback whale 'spy-hopping' at the former whaling ground in Moreton Bay, Queensland, with Cape Moreton in the background. (Photo, Moreton Bay Whalewatching)

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# A REVIEW OF HUMPBACK WHALE CATCHES BY MODERN WHALING OPERATIONS IN THE SOUTHERN HEMISPHERE

K.P. FINDLAY

Findlay, K.P. 2000 12 31. A review of humpback whale catches by modern whaling operations in the Southern Hemisphere. *Memoirs of the Queensland Museum* 47(2): 411-420. Brisbane. ISSN 0079-8835.

Catches of humpback whales in the Southern Hemisphere are reviewed from a number of sources, along with numbers of catcher vessels which operated on each whaling ground, where data were available. Catches amounted to >200,000 whales and can be divided into four groups: 1) pre-1917 coastal whaling from shore stations and floating factories; 2) Antarctic and low latitude pelagic and coastal catches reported to the Bureau of International Whaling Statistics (1923-1963); 3) post-1942 coastal catches largely centred in Australian and New Zealand waters; and 4) other catches, including those of the *Olympic Challenger* and the Soviet Antarctic whaling fleets. Crude catch per unit of effort (CPUE) indices were calculated as annual catch per catcher vessel for the Falkland Island Dependencies, African and South American whaling grounds. No CPUE indices could be calculated for the Australian grounds or the Antarctic pelagic whaling grounds. Catch trends in most grounds showed marked declines within the first decade of whaling, followed by no recovery. Marked differences in catch trends off both Gabon and Madagascar from those of other grounds off the west and east coasts of Africa respectively, suggest stock segregation in both areas. □ *Humpback whale, catches, Southern Hemisphere, modern whaling.*

K.P. Findlay, Oceanography Department, University of Cape Town, Rondebosch 7701, South Africa; 1 September 2001.

Southern Hemisphere humpback whales (*Megaptera novaeangliae*) undertake annual migrations from summer polar feeding grounds to winter breeding grounds in tropical and sub-tropical waters (Risting, 1912; Olsen, 1914; Harmer, 1929, 1931; Matthews, 1938; Mackintosh, 1942). Seven feeding grounds have been identified within the Southern Ocean (Mackintosh, 1942; Omura, 1973; International Whaling Commission, 1998), each linked to a breeding ground in coastal waters of either South America, Africa (including Madagascar), Australia, New Zealand or the islands of the southwestern Pacific Ocean (Kellogg, 1929; Rayner, 1940; Mackintosh, 1942; IWC, 1998). En route between breeding and feeding grounds humpback whales utilise the coastal waters of Southern Hemisphere continents as migratory corridors, a factor which made them susceptible to coastal whaling in tropical and sub-tropical waters from the first decade of the 20th Century.

Pre-exploitation size of the Southern Hemisphere humpback whale population was estimated at 90,000-100,000 (Chapman, 1974). Based on sightings in the Antarctic between 1933-1939, Mackintosh & Brown (1965) estimated the combined southern population of blue (*Balaenoptera musculus*), fin (*Balaenoptera physalus*) and humpback whales at 220,000 with a range of

142,500-340,000. Chittleborough (1965), using an estimate of 220,000-340,000 whales, and Mackintosh's (1942) assumption that 10% of the large baleen whales in the southern oceans were humpback whales, suggested that the Southern Hemisphere humpback whale population was in the order of 22,000-34,000 between 1933-1939.

## MATERIALS AND METHODS

Brief descriptions of operations in each of a number of whaling grounds were sourced from the Bureau of International Whaling Statistics (BIWS, 1942-1964), Tønnesen & Johnsen (1982), Dawbin (1956), Best (1994), Best & Ross (1989), Goodall (1913), Chittleborough (1965), Williamson (1975), Budker (1954), Budker & Collignon (1952), Angot (1951), Olsen (1915), Ommaney (1933), Risting (1912), Omura (1973), Grady (1982), Hinton (1925), Barthelmess et al. (1997), Mackintosh (1942) and Zemsky et al. (1997).

Time series of catches from different localities were compiled from the BIWS (1942-1964), Best (1994), Dawbin (1956), Chittleborough (1965), Grady (1982) and Tønnesen & Johnsen (1982). Numbers of whale catcher vessels operating each year were obtained from the BIWS (1942-1964) for some whaling grounds and were used to calculate crude catch per unit of effort (CPUE)



indices, as catch per number of catcher vessels per annum. Indices were calculated for the Falkland Island Dependencies, southern African coasts, southern American coasts and Kerguelen Island. These CPUE indices must be considered crude and may be biased by environmental conditions (e.g. ice and weather), catch selectivity, differences in catcher vessel tonnage, operational limitations (including towing of carcasses to stations, availability of water) and catch regulations. No attempt was made to quantify these possible biases.

Given a series of catches ( $c$ ) and associated catch effort ( $e$ ) over time ( $t$ ), the catch per unit effort ( $C$ ) was calculated (as  $c/e$ ). In the time series available,  $C$  generally decreases over time. Given the following assumptions, the decline in catch per unit effort (CPUE) can be assumed to reflect the extent of depletion (De Lury, 1947): 1) catchability of animals (the proportion of population caught by one unit of effort) is constant between seasons; 2) unit of effort is constant between seasons; and 3) the population is closed.

Under these assumptions, De Lury (1947) suggested that:

$$\log C = \log (kN_{(0)}) - kE \quad \text{and,} \\ C = k(N_{(0)} - K),$$

where  $E$  and  $K$  are the total effort and total catch, up to interval  $t$ , and  $N$  is the number of individuals in the population at time  $t$ . Plotting both the catchability ( $k$ ) and the initial stock size prior to catching,  $N_{(0)}$  can be estimated by elementary regression analyses of  $C$  against  $K$ . Regression analyses (of  $C$  against  $K$ ) were carried out for the Falkland Island Dependencies and the African west coast (excluding Gabon), Gabon, and east coast (excluding Madagascar). The three assumptions may be seriously violated by biases in the CPUE indices expressed above as well as the open nature of the populations due to natural mortality and recruitment, and any changes in migration patterns over time.

*Season Notation.* In this text, year combinations such as '1910/1911' indicate a Southern Hemisphere summer season.

## RESULTS

**CATCH HISTORIES.** Total catches for the areas north and south of 40°S are presented in Tables 1 and 2 respectively. Catches from South America are included in Table 1 regardless of latitude.

**THE FALKLAND ISLAND DEPENDENCIES.** Modern whaling of humpback whales in coastal

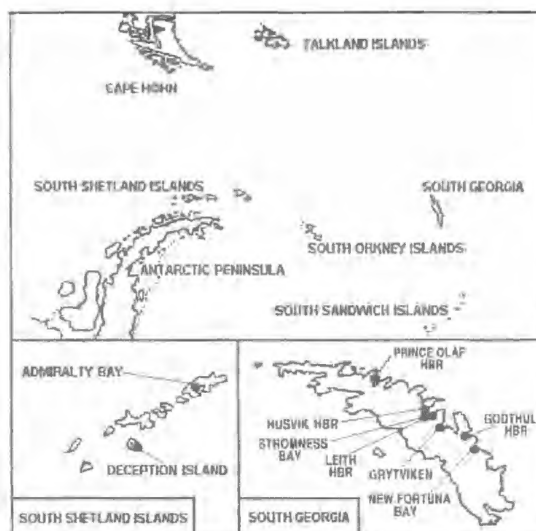


FIG. 1. Locations of shore-based modern whaling stations in the Falkland Island Dependencies.

waters of South Georgia operated from 1904-1955. Shore stations were established at Grytviken (1904-1962), Husvik Harbour (1907-1961), Stromness Bay (1907-1931), Leith Harbour (1909-1955), Godthul Harbour (1908-1929), New Fortuna Bay (1909-1920) and Prince Olaf Harbour (1911-1931) (Fig. 1). Moored floating factories were used at Husvik Harbour (1907-1911), at Stromness Bay (1907-1912) at Prince Olaf Harbour (1911-1916) and at Godthul Harbour (1908-1929) (Fig. 1). Catches of humpback whales were banned in the waters of South Georgia from the summer 1918/19 season, although some animals were taken each year between 1918-1921. This ban was reinforced in 1921, although relaxed by 1926/1927.

Whaling at the South Shetland Islands started in 1905/1906 when the floating factory *Admiralen* spent one month whaling in Admiralty Bay at King George Island. In 1906 the harbour at Deception Island was discovered and this became the centre of whaling at the South Shetland Islands. Catches prior to 1909/1910 were not well documented.

Whaling at the South Orkney Islands began in 1907/1908, although sea ice resulted in the operation being moved to the South Shetland Islands within this season. In 1911/1912 a floating factory with two catcher vessels operated in the region. Abundant stocks of blue and fin whales and adequate water and anchorage saw four floating factories (with six catcher vessels)

TABLE 1. Low latitude catches (north of 40°S) of Southern Hemisphere humpback whales by modern whaling between 1904 and 1974.

Location	Catch
Southern Africa (Total)	47134
Cape	1571
Namibia	1284
Angola	10027
Gabon	15158
Natal	9785
Mozambique	3128
Madagascar	6181
South American East Coast	1557
South American West Coast	1985
Australian West Coast	19557
Australian East Coast	8307
New Zealand	5224
Low Latitude Pelagic Whaling (Total)	9612
West Australia	7243
Gabon	2309
Peru and Chile	70
<i>Olympic Challenger</i> Fleet	105

operating the following season. Three of these returned in 1913/1914, but results were so poor that only one remained in 1914/1915. Conditions at the South Orkney Islands were difficult due to ice formation from the Weddell Sea and the season was limited to 2-3 months a year. Such difficulties with ice formation in 1912/13 resulted in whales being caught along the ice barrier, the first attempts at 'pelagic whaling' in the Antarctic. Tønnessen & Johnsen (1982) note that whaling off the South Orkney Islands was important as it: proved that it was possible to operate within the pack ice; placed the idea of a slipway into practice; and generated considerable information on the relationship between ice, plankton and whale stocks.

Initially whaling at the South Sandwich Islands was limited to one season, 1911/1912, when 28 whales were caught. This was a failure and attempts were not repeated. Although seven licences were issued for whaling in the region, six licencees withdrew on hearing of the difficult conditions encountered by the other company. However, Tønnessen & Johnsen (1982) noted that in the 1920's many floating factories operated near the islands.

Whaling in the Falkland Islands started in 1905/1906 as expeditions to the South Shetland Islands visited en route to and from the whaling grounds.

TABLE 2. High latitude catches (south of 40°S) of Southern Hemisphere humpback whales by modern whaling between 1904 and 1974.

Location	Catch
Land Stations & Floating Factories (Total)	34683
South Georgia	24770
South Shetland Is	8879
South Orkney Is	405
Falkland Is	200
Kerguelen Island	429
Antarctic Pelagic Whaling (Total)	25393
Area I	1295
Area II	1537
Area III	7074
Area IV	11988
Area V	2405
Area VI	1094
<i>Olympic Challenger</i> Fleet	4554
Soviet Antarctic Whaling Fleet (Total)	48724
Area I	414
Area II	1364
Area III	1280
Area IV	2638
Area V	4861
Area VI	3332
Unknown	34835

A total of 34,265 humpback whales was taken from land-based stations and moored floating factories in the Falkland Island Dependency region between 1904-1963 (Table 2). Humpback whales formed the bulk of catches during the initial years (until 1914/15), peaking in 1910/1911 when 8,294 were taken. By 1916 catches had declined considerably (only 131 humpback whales were taken in the Antarctic in 1916/17), although their increasingly secondary importance to catches of blue whales must be noted. Catches of humpback whales from land stations in the Falkland Island Dependencies remained low until ceasing at South Georgia in 1955.

**AFRICAN COAST.** Modern whaling in South Africa began at Durban in 1908 after reports of the abundance of whales were received in Norway. By 1909 floating factories were operating off the west coast at Saldanha Bay. The success of the entrepreneurial whaling companies in south Africa in 1909 and 1910 resulted in a whaling boom in the region. By 1913, 11 floating factories and 17 land stations were in operation between Gabon (French Congo) and Mozambique (Portuguese East Africa), during which an estimated 7,263 humpback whales were

taken. The distribution of shore-based modern whaling stations on the southern African coast is shown in Fig. 2 (after Best, 1994).

Modern whaling in the waters of Madagascar probably began in the 1910 winter, although poor catches in 1912 resulted in abandonment by whaling fleets. Catches from this era are unknown. Humpback whales were caught to the south of Madagascar during the 1937 and 1938 seasons, and although the exact location of these catches are not specified by the BIWS, Budker (1954) noted they were some distance to the south of Madagascar. Such catches may have been from the Walters Shoal area where Best et al. (1998) have reported sightings of humpback whales. A further bout of humpback whale catches occurred off Madagascar in 1949-1950 (Angot, 1951).

Best (1994) estimated that over 31,000 humpback whales were taken off the southern African coast (excluding Madagascar) from 1908-1930, although there is still some uncertainty on the early catches off Angola, Mozambique and Gabon. As with catches in the Falkland Island Dependencies, humpback whales were the initial target, although by 1915 blue whales had become a higher priority. A total of 47,134 humpback whales was taken by modern land-based stations and moored floating factories off the southern African coast between 1908-1963, with 28,040 and 19,094 of these taken off the east and west coasts respectively (Table 1). A further 2,309 were taken by low latitude pelagic whaling fleets operating off Gabon (Table 1).

**KERGUELEN.** One Norwegian company (A/S Kerguelen) was granted a licence in 1908 for whaling and sealing of elephant seals in the waters of Kerguelen Islands. Whale catches were poor and although abandoned in 1911, sealing continued until 1914. A total of 429 humpback whales were taken during this time.

**SOUTH AMERICA.** Levels of whaling on the east and west coasts of South America were insignificant compared with levels at other continents (Tønnessen & Johnsen, 1982). The first humpback whale to be taken by modern whaling in the Southern Hemisphere was caught in the Straits of Magellan on New Year's Eve in 1903, and by 1905 a whaling station had been established at Punta Arenas in Chile. The success of this station resulted in the formation of a Chilean whaling company (Sociedad Ballenera de Magallanes) which operated at Deception Island (South Shetlands) in 1906. In 1906 a further company was established at Valdivia in

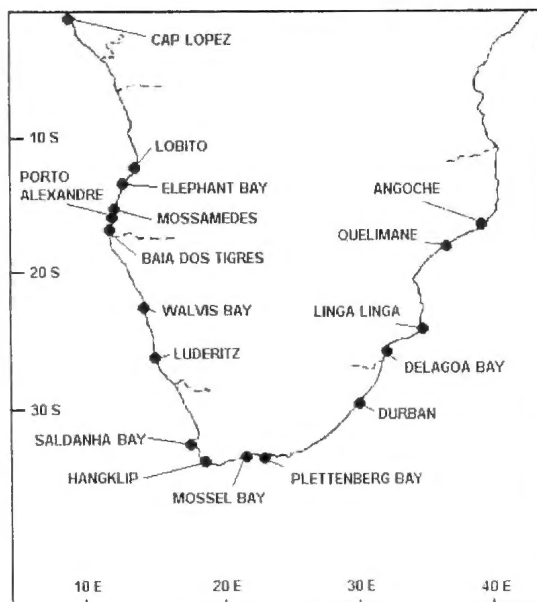


FIG. 2. Locations of shore-based modern whaling stations on the southern African coast (after Best, 1994).

Chile from where a shore station and a floating factory ship were in operation until 1913. In 1914 the floating factory *Sabraon* followed the northward migration of whales along the coasts of Chile, Peru, Ecuador and Colombia and caught 327 whales (almost exclusively humpback whales) over the period April 1914 - May 1915. The two companies were sold to the Sociedad Ballenera Corral S.A., just south of Valdivia, in 1913 and 1917 respectively.

Modern whaling of humpback whales in Brazil started at Costinha in 1910 (Williamson, 1975) or 1911 (Tønnessen & Johnsen, 1982). In the following year three companies were operating, one Brazilian and two Norwegian. By 1913 and 1914 the Norwegian companies had terminated operations. A second shore station was established at Cabo Frio in 1960, while modern whaling was carried out from Santa Catarina from 1952. It appears that the majority of humpback whale catches were made from the Costinha station.

Totals of 1,557 and 1,985 humpback whales were taken by modern whaling off the east and west coasts of South America respectively (Table 1). Catch records for Brazil are incomplete between 1929-1946 however, and possibly unreliable in certain other years. No attempt has been made to include the early 1905/1906 catches from southern Chile for which no species

identifications could be sourced. These totals in all likelihood include the 327 whales (almost exclusively humpback whales) taken by the floating factory *Sahraon* which operated off the coasts of Chile, Peru, Ecuador and Colombia in 1914.

**AUSTRALIA (INCLUDING NORFOLK ISLAND) AND NEW ZEALAND.** In 1909 the Norwegian consul in Sydney drew Norwegian whalers' attention to the abundance of whales in Australian waters, and by 1911 ten companies expressed interest in whaling operations. Of these, four never commenced, two operated on an experimental basis in 1912, one operated a floating factory at Jervis Bay, New South Wales between 1912-1913, while three co-operative companies operated at Albany and Point Cloates (Norwegian Bay) in Western Australia from 1912-1916. By 1913, authorities in Western Australia introduced catch regulations (Tønnessen & Johnsen, 1982) and the three co-operatives closed in 1916. The Point Cloates station operated again between 1922-1928, although profitable catches were only recorded after 1925 (Tønnessen & Johnsen, 1982). Shore-based whaling resumed in 1949 on the west coast, after a period of extensive whaling in Western Australian waters by foreign fleets between 1935-1939 (BIWS, 1964). Shore-based operations after 1949 were at Point Cloates (1949-1955), Carnarvon (1950-1963) and Albany (1952-1963) on the west coast and at Tangalooma (1952-1962) and Byron Bay (1954-1962) on the east coast and at Norfolk Island (1956-1962) (Chittleborough, 1965) (Fig. 3).

Modern whaling began in New Zealand in 1910 when a modern catcher vessel was acquired at Whangamumu, although a net fishery for humpback whales had operated there between 1893-1910 (Ommanney, 1933; Dawbin, 1956). A number of humpback whaling centres existed in New Zealand after 1911: Whangamumu (which closed in 1931); Kaikoura between 1917-1922; and in the Tory Channel of Cook Strait (including the Perano station) which took humpback whales until 1963 (Grady, 1982) (Fig. 3). Catching of humpback whales at the Tory Channel station was carried out from small (34ft) fast vessels operated by crews of two rather than from conventional catcher vessels. Light harpoons were fired from a small 32mm cannon to capture the animal, whereafter it was dispatched by explosive shell detonated from the catcher vessel.

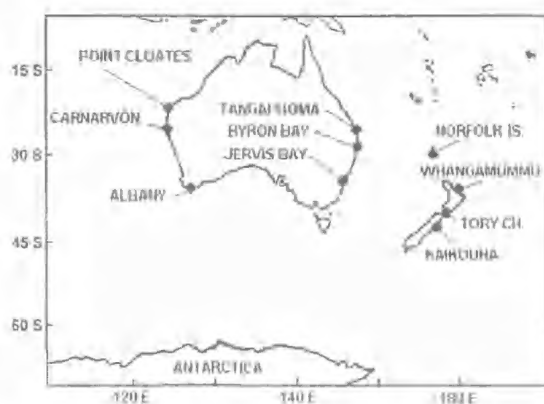


FIG. 3. Locations of shore-based stations in Australia and New Zealand.

Totals of 19,557 and 8,302 humpback whales were taken by modern land-based stations and moored floating factories off the west and east coasts of Australia respectively between 1911-1963 (Table 1). A further 1,870 whales taken in 1912 and 1913 were reported to the BIWS as from the coast of Australia and could not be allocated to a specific locality. A further 7,243 humpback whales were taken by foreign fleets off the west coast between 1935-1939 (Table 1). Catches on both coasts after 1949 were subject to annual quotas, which were met up until 1957 on the west coast and 1961 on the east coast. Chittleborough (1965) noted a rapid decline in catch per unit effort during this period and suggested, at least in the case of the east coast stock, that this may have arisen from substantial undeclared catches.

A total of 3,923 humpback whales were reported by Dawbin (1956) to have been taken by modern whaling (including the Perano's small boat whaling) in New Zealand waters between 1912-1955. A further 1,601 were taken in the Tory Channel between 1956-1963 resulting in a total catch of 5,524 humpback whales (Table 1).

**ANTARCTIC PELAGIC WHALING.** Pelagic whaling began in the Antarctic with a single season off the South Orkney Islands in 1912 and again in the Ross Sea in 1923/1924. Humpback whale catches over the period 1934-1938 were large and consequently the species was protected from pelagic whaling in Antarctic waters from 1938-1949 by the International Agreement for the Regulation of Whaling (ARW). A temporary relaxation of this protection in 1940/1941 resulted in a catch of 2,675 while catches by the Japanese (who at the time were not members of the ARW)



in 1938/39 accounted for a further 883. From the 1949/1950 to the 1951/52 seasons, catches of humpback whales to the south of 40°S (and outside of the declared sanctuary of 70°-160°W) were limited to 1,250 each year, with a four-day grace period set after this catch was achieved. However, catches during the four-day grace period were high and from 1952/1953, catches of humpback whales in Antarctic waters were regulated by a limited (four day) season over the period 1-4 February. The 70°-160°W sanctuary remained in place until 1955/1956 and from 1954/1955 the waters south of 40°S and between 0°-70°W were closed to humpback whaling. From 1958/1959 the western boundary of this area was shifted east to 60°W.

A total of 25,393 humpback whale catches were reported to the BIWS by Antarctic pelagic whaling fleets between 1923-1963 (Table 2). This excluded the falsified Soviet catches reported to the BIWS between 1948/1949 and 1972/1973 (Zemsky et al. 1997, in IWC, 1997).

**THE OLYMPIC CHALLENGER CATCHES.** The Olympic Whaling Company S.A., registered in Montevideo, Uruguay, operated the *Olympic Challenger*, a Panamanian registered floating factory and twelve whale catcher vessels, some of which were registered in Honduras. As neither nation had ratified the Washington Convention the owners saw fit to ignore regulations. The *Olympic Challenger* whaling fleet operated in Antarctic waters and off the west coast of South America between 1950/1951 and 1955/1956 (excluding 1953/1954). Barthelmess et al. (1997) stated that it had long been noted that major discrepancies existed between the catch records submitted to the BIWS and true catch records, and provided an approximation to the true catch figures. Such approximated catch figures have been used in this review.

A estimated 4,554 humpback whales were taken in the Southern Ocean by the *Olympic Challenger* fleet between December 1950 and April 1956 (Table 2). A further 105 were taken off the west coast of South America in the winter of 1954 (Table 1).

**SOVIET ANTARCTIC WHALING FLEETS.** The Soviet Union operated four Antarctic whaling fleets between the 1946/47 and 1986/1987 seasons. The *Slava* fleet operated from 1946/1947 until 1965/1966; the *Sovietskaya Ukraina* fleet between 1959/1960 and 1986/1987; the *Yurii Dolgurukiy* fleet between 1960/1961 and 1974/1975; and the *Sovietskaya Rossia* fleet

between 1961/1962 and 1979/1980. Catches of humpback whales reported to the BIWS (in terms of Article VII of the International Convention for the Regulation of Whaling, 1946) were unreliable for the period 1948/1949 to 1971/1972 (Yablokov, 1994) and reported and true catches were presented by Zemsky et al. (1997, in IWC, 1997). Daily (noon) catch positions are known for only a portion of the *Slava*, *Sovietskaya Rossia* and *Sovietskaya Ukraina* catches, while positions of the *Yurii Dolgurukiy* were known only by IWC Areas.

Despite reporting a total catch of 2,700 humpback whales to the BIWS (in terms of Article VII of the International Convention for the Regulation of Whaling, 1946), the Soviet Antarctic whaling fleet caught 48,724 humpback whales between 1948/1949 and 1972/1973 (Table 2). Of these, 34,835 have no associated locality, while the remainder are designated by IWC Management Area (Table 2). It must be noted that a small percentage of these whales were possibly taken in the northern Indian Ocean or north of 40°S as reflected in the figures of catch positions of all species presented by Mikhalev (1997, in IWC, 1997).

#### CATCH PER UNIT EFFORT AND 'DE LURY' ANALYSES

Crude CPUE indices have been calculated for the Falkland Island Dependencies, the Southern African coasts, the South American coasts and Kerguelen Island from total catch and total effort (expressed simply as number of operating catcher vessels) per year (Fig. 4A-D).

Plotting of CPUE against total catch provides an estimate of pre-exploitation population size (De Lury, 1974). This has been carried out for the initial years of whaling in Falkland Island Dependencies (1904-1918), the African west coast excluding Gabon (1909-1920), the African east coast excluding Madagascar (1908-1918), and Gabon (1910-1912) (Fig. 5A-D). Results of simple regression of CPUE against total catch suggest initial stock sizes of 34,700 for the Falkland Island Dependencies, 13,600 and 8,600 for the African west (excluding Gabon) and east Coasts (excluding Madagascar) respectively, and 8,400 for the whaling grounds of Gabon. Given the biases in CPUE indices and the crude nature of the effort, these estimates should be regarded with caution. The open nature of the populations in consideration would result in these estimates being biased upwards.

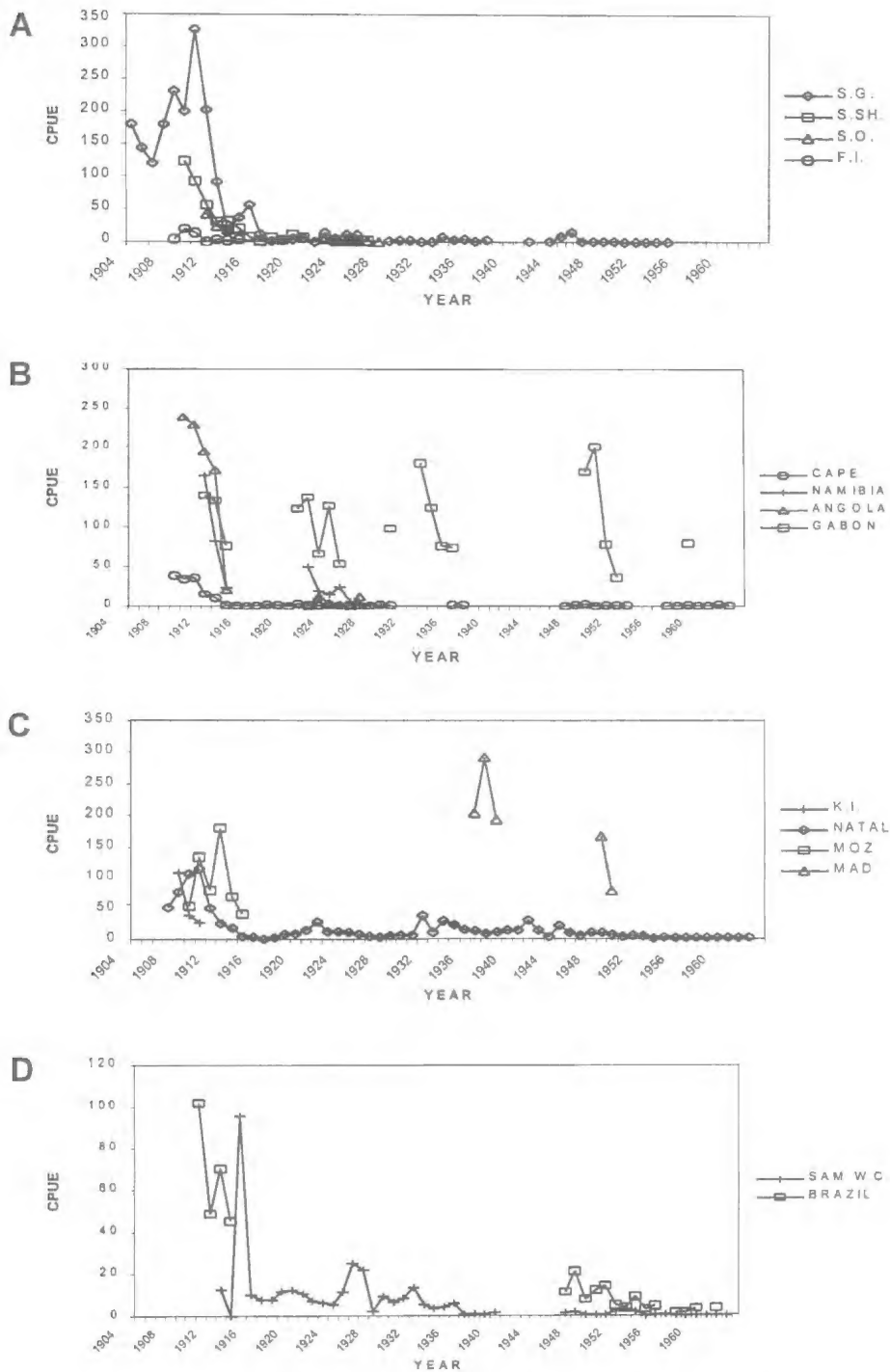


FIG. 4. Annual catch per number of catcher vessels (CPUE) from modern whaling grounds off: A, Falkland Island Dependencies; B, southern African west coast; C, southern African east coast and Kerguelen Island; and D, South American coasts. S.G. = South Georgia; S. SH. = South Shetland Islands; S.O. = South Orkney Islands; F.I. = Falkland Islands; K.I. = Kerguelen Island; MOZ. = Mozambique; MAD. = Madagascar; SAM. W.C. = South American West Coast.

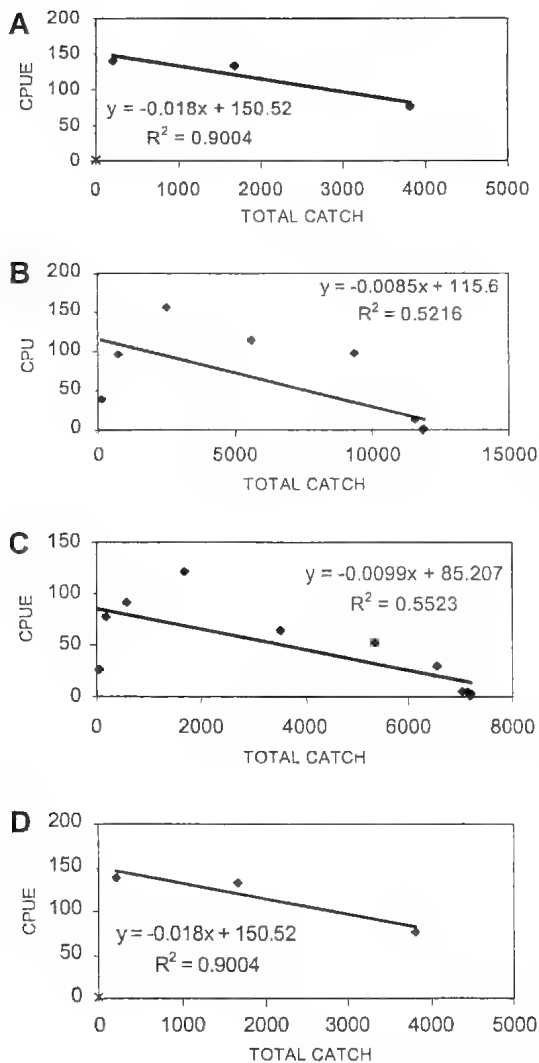


FIG. 5. Simple regression of catch per unit effort (CPUE) against total catch for: A, Falkland Island Dependencies 1904-1918; B, African west coast (excluding Gabon) 1909-1920; C, African east coast (Natal and Mozambique) 1908-1918; and D, coast of Gabon 1912-1914.

## DISCUSSION

Catches of Southern Hemisphere humpback whales by modern whaling since the beginning of the 20th Century amount to over 200,000 and can be divided into four major eras: 1) pre-1917 coastal whaling from shore stations and floating factories; 2) Antarctic pelagic catches reported to the BIWS; 3) post-1942 coastal catches largely centred in Australian and New Zealand waters;

and 4) other catches made by the *Olympic Challenger* and the Soviet Antarctic whaling fleets.

Catch trends of humpback whales in particular whaling grounds appear to follow two basic patterns. In multi-species whaling grounds (where humpback whales would have been taken non-selectively, or grounds where humpback whales were caught elsewhere during migration), catch per unit effort declined markedly in the initial years and remained low until the cessation of whaling. However, in single species grounds (where catch effort was only directed at humpback whales), catches per unit effort may have declined to levels where whaling was no longer economically viable, leading to the closure of operations. In such species whaling grounds (e.g. off Gabon and possibly Madagascar) the closure of whaling appeared to allow some stock recovery.

Of particular interest is the difference between the catch series off Gabon and other locations on the west coast of Africa. Catches off the Cape, Namibia and Angola (as multi-species grounds or where humpback whales migrated through other whaling areas) declined markedly in the initial years of whaling and remained low until the IWC ban in October 1963. Catches off Gabon, however, declined in the initial period and as a single species whaling ground, the decline in humpback catches resulted in closure of operations. It appears that such closure allowed some recovery of the Gabon 'stock' and whaling resumed, again resulting in declines. CPUE indices from the end of each of the four whaling periods on the Gabon grounds have been projected at 10% per annum to the commencement of the next periods (Fig. 6). These projections suggest that recovery of the Gabon population, in each of the four successive eras, may well have been similar to increase rates of about 10% described elsewhere in the Southern Hemisphere (Paterson & Paterson 1989; Paterson et al. 1994, 2001; Bannister, 1994; IWC, 1996). Four such cycles are apparent in the Gabon catch history, but not in the catch histories from the other grounds on the west coast of southern Africa. Possibly whales from Gabon did not migrate through other grounds or to the Antarctic, suggesting possible stock segregation of humpback whales in this region. If so, then the question remains as to where humpback whales that winter on the Gabon grounds migrate to in summer. Summer incidence of humpback whales on temperate or tropical and sub-tropical low latitude feeding grounds associated with



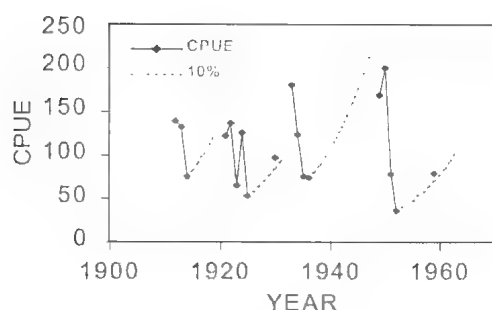


FIG. 6. Projection of a 10% increase in catch per unit effort indices from the whaling grounds off Gabon from the end of each whaling period to the initiation of the next.

upwelling areas has been noted (Papastavrou & van Waerebeek, 1997; Findlay & Best, 1995). Although no summer records of humpback whales could be sourced for the area, upwelling does occur in the Gulf of Guinea and in the region of the mouth of the Congo River.

Similarly, there appears to be considerable difference in the CPUE indices between the Mozambique (and KwaZulu-Natal, as Mozambique humpback whales are assumed to pass through the Durban whaling grounds en route to and from Mozambique) and Madagascar whaling grounds suggesting some stock segregation within the southwestern Indian Ocean. Best et al. (1998) noted that humpback whale catches off the Durban and Mozambique whaling grounds had declined by 1915, yet Angot (1951) noted that by the end of the 1950 whaling season, stocks around Madagascar had been significantly reduced to such an extent that commercial exploitation was no longer viable.

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# EXPLOITATION OF HUMPBAC WHALES, *MEGAPTERA NOVAEANGLIAE*, IN THE SOUTH WEST PACIFIC AND ADJACENT ANTARCTIC WATERS DURING THE 19TH AND 20TH CENTURIES

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European discovery of the South West Pacific is briefly described in the context of subsequent whaling. Exploitation of humpback whales *Megaptera novaeangliae* in that region and adjacent Antarctic waters is considered in detail. Catches in the era of sail during the 19th Century were followed by extreme over-exploitation in the modern whaling era, particularly in the middle third of the 20th Century. Whaling methods in the different periods are discussed. □ *History of humpback whaling, 19th and 20th Century, South West Pacific, Antarctic waters.*

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The Pacific Ocean was named in 1520 by Ferdinand Magellan, who entered it after passing through the South American straits by which he is immortalised (Hough, 1971). Exploration of this vast ocean by British, Dutch, French and Spanish navigators continued during the 17th and 18th Centuries but two, Abel Tasman and James Cook, stood above the rest. Tasman discovered Van Diemen's Land (Tasmania), New Zealand, Tonga and Fiji in 1642-43 and Cook in three voyages from 1768-79 discovered inter alia the strait, which bears his name, separating the north and south islands of New Zealand and the east coast of Australia, including the Great Barrier Reef (Fig. 1). Cook was the first to cross the Antarctic Circle reaching 71°10'S in 1774, a record which stood for 50 years. He was killed at Hawaii in 1779. Hartley Grattan (1963) noted: 'With his death a great and marvellous era in the history of exploration was closed. All that happened after in Pacific exploration was like an epilogue'. However, Moorehead (1966) noted in his account of the European invasion of the South Pacific: '... it was Cook's fate to bring disaster in his wake. He had stumbled upon what was probably the largest congregation of wild life that existed in the world, and he was the first to let the world know of its existence'. Exploitation of but one species of marine mammal, the humpback whale *Megaptera novaeangliae*, in the South West Pacific and adjacent Antarctic waters in the two centuries following Cook's discoveries is the subject of this paper.

In 1789 the whaleship *Emilia* owned by Enderby & Sons of London entered the Pacific

via Cape Horn (Dakin, 1934). Small numbers followed in the last decade of the 18th Century but an avalanche occurred in the 19th. Vessels carrying the flags of Britain (including the recently settled east coast of Australia), France, Holland, Portugal and the United States of America predominated, particularly the latter. Richards (1988) also noted the loss of the *Mozart* of Bremen with a cargo of sperm whale oil at Christmas Island in 1847. The sperm whale, *Physeter macrocephalus*, was widely hunted and the southern right whale, *Eubalaena australis*, was almost exterminated from the high-seas and the bays and inlets of southern Australia. New Zealand and its adjacent sub-Antarctic islands (Dakin, 1934; Dawbin, 1986). In the early part of the 19th Century, waters to the south of New Zealand and Australia were also the province of sealers. Whale exploitation in the far south, including the Antarctic sea entered by James Clark Ross in 1841 (Mountfield, 1974), occurred in the 20th Century after the era of sail had given way to steam.

## OPEN BOAT AND NET WHALING

**PELAGIC WHALING.** The benchmark for 19th Century humpback whale captures in the South West Pacific is Chart D of Townsend (1935). From the available logs of American whaleships the position on a day when one or more whales were captured was indicated and colour coding enabled determination of the month of capture. Clustering and overlap create difficulty in assessing regional captures but estimates (and a monthly breakdown) for the major capture sites

in the South West Pacific are as follows: Tonga 375 (July 20, August 124, September 107, October 24); Chesterfield Reefs 98 (July 18, August 47, September 33); Three Kings Island 29 (July 4, August 13, September 12); Cook Strait 28 (May 10, June 8, July 5, August 5); Foveaux Strait 8 (May 3, June 1, July 2, August 2). Captures were also recorded from Fiji, Norfolk and Lord Howe Islands (Fig. 1) as well as high-seas areas. American humpback whaling operations were also conducted in Samoan waters and the French operated in New Caledonian waters in the mid 19th Century (Garrigue & Gill, 1994). No humpback whale captures were recorded inside the sheltered waters of the Great Barrier Reef now a well documented calving ground (Paterson & Paterson, 1984, 1989; Simmons & Marsh, 1986; Paterson, 1991). It is possible that the near disaster experienced by Cook in 1770 when his vessel struck a reef near the mouth of the subsequently named Endeavour River may have deterred whaling in that region.

Given that the certainty of humpback whale migration habits was recognised as early as 1857 (Mitchell & Reeves, 1983), it is of note that the species was not a more common target of pelagic whalers. The majority of 19th Century humpback whale captures were made in the 50's to mid 80's following the great decline in right whale populations (Townsend, 1935; Wray & Martin, 1983). Wray & Martin also noted that humpback whales yielded high grade oil but Mitchell & Reeves (1983) disputed this and quoted various authorities indicating general market preference in most years (although not in the 80's) for sperm whale oil. Bullen (1901) mentioned that poor catches of humpback whales were compensated for by the peacefulness of a visit to the nearby Friendly Islands. Ambivalence regarding capture of the species is discussed by Mitchell & Reeves (1983) who, together with Wray & Martin (1983), noted that male humpback whales were difficult to catch and this resulted in concentrated effort on cows accompanied by calves. Accordingly, it is likely that captures recorded by Townsend (1935) in areas such as Tonga and the Chesterfields (Fig. 1) during the austral spring may have resulted in 'double mortality' given that those regions were known calving grounds and that orphaned calves would have had little chance of survival. The possible long term result of this practice (banned by international agreement in 1931, effective in 1935) on humpback whale populations in the South West Pacific will be discussed later but it should be noted that

similar exploitation was to occur in the Tongan region, albeit at a low rate, for another century (Ruhen, 1966).

**TWOFOLD BAY.** Situated at 37°S on the east Australian coast (Fig. 1), Twofold Bay is remarkable in Australian whaling history for two reasons. Firstly, whaling by traditional (open-boat and shore-based) methods extended for a period of ~70 years until the late 1920's and secondly, it is the only recorded site of cooperation between killer whales *Orcinus orca* and man with regard to whale capture.

An early reference to humpback whaling at Twofold Bay, associated with the collapse of the southern right whale population, was noted in correspondence between James Hewitt and James Kelly, an Australian whaling pioneer. Hewitt was sent in the *Amity* from Hobart to Twofold Bay in 1841. The expedition was disastrous and no right whales were seen from 24 June to 31 August. Hewitt returned with oil from only 6 small humpback whales (Bowden, 1964). The southern right whale industry from the many but small Tasmanian shore stations had collapsed by 1845. It is probable that small numbers of humpback whales were taken in that period.

The long period of humpback whale exploitation at Twofold Bay by traditional methods was dominated by the Davidson family who operated a small station at the mouth of the Kiah River from 1866 until about 1927 (Dakin, 1934; Davidson, 1988). Annual catches are difficult to determine but a catch of 20 in a season (June–November) was considered to be exceptionally high and in some years, particularly in the 20th Century, none were caught (Davidson, 1988). It should be mentioned that the Davidsons captured other species, including occasional right whales and a 24.4m long blue whale, *Balaenoptera musculus*, in 1910, a record for traditional methods. As was the practice of the American pelagic whalers, the Davidsons killed cows accompanied by calves as the following account (which also documents killer whale cooperation) demonstrates: 'On Tuesday [4 November 1919] a large humpback whale and calf ... coerced by killers, came into the harbour, where they were effectually held up under a fierce attack by their pursuers pending the arrival of the Kiah whalers. In due course George Davidson got home with the harpoon and, after a lengthy chase which was followed by a large number of highly interested and excited spectators, succeeded in securing his prize ... The calf was allowed to escape, and the

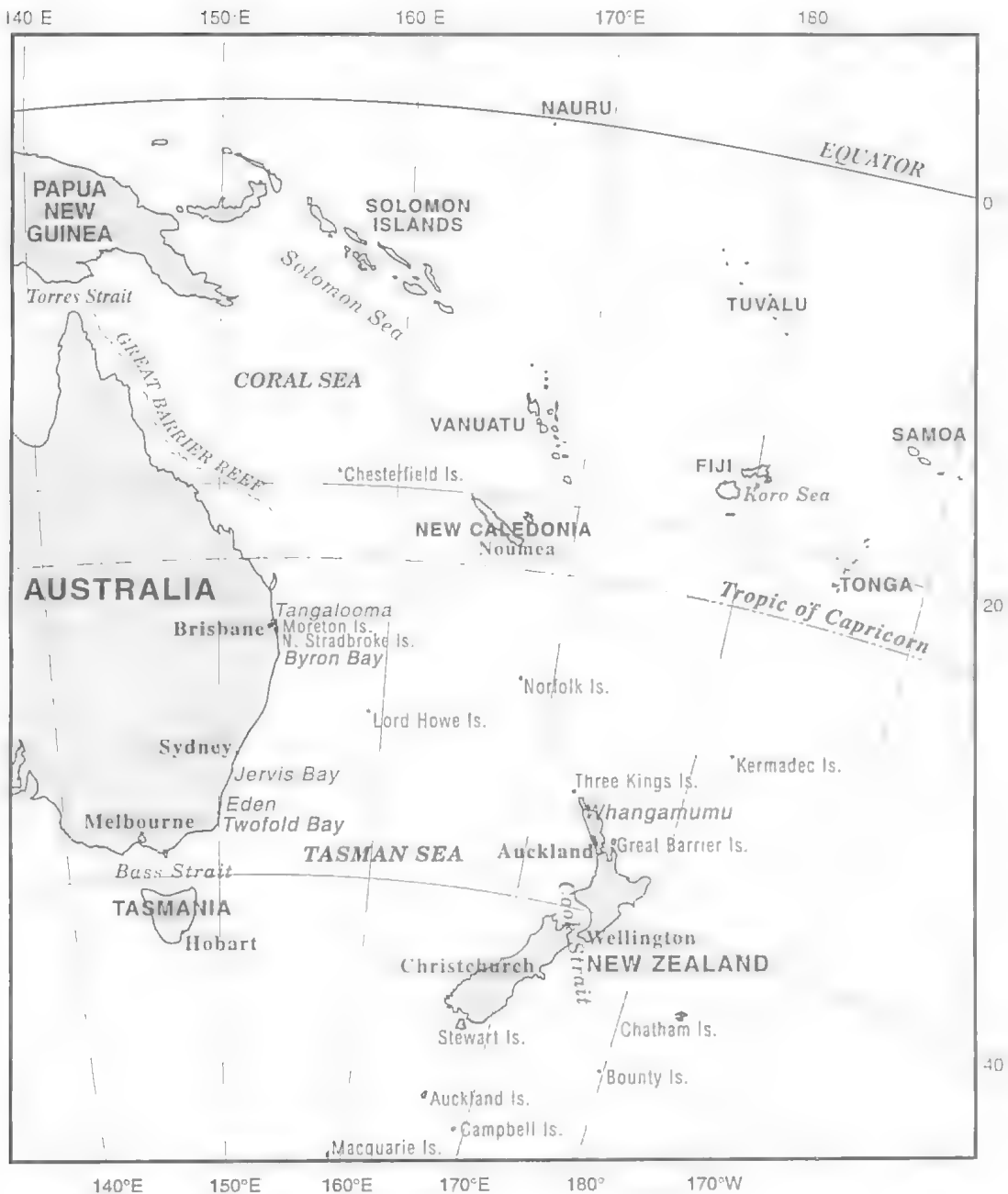


FIG. 1. Map of the South West Pacific Ocean.

next morning followed the dead body of its mother as the latter was being towed to the whaling station at Kiah River.' (Davidson, 1988). The reference to the mother being towed to the whaling station the day after being killed reflected the practice at Twofold Bay, which was similar to that of pelagic humpback whaling, of

waiting for the whale to bloat before processing commenced. In contra-distinction to right whales, humpback whales sank when killed and rose to the surface as decomposition advanced. In the context of Twofold Bay, the resultant buoyancy allowed for easier towing by rowing boats to the station.

The role of killer whales at Twofold Bay was described as early as 1843 by Oswald Brierly and their habit of driving humpback whales (as well as other species) into the bay and 'keeping' them there in anticipation of being rewarded by the whalers with choice pieces, preferably the tongue, has been described by many authors, including Dakin (1934) and Mead (1963). Mitchell & Baker (1980) comprehensively documented this unusual behaviour.

**NEW ZEALAND AND NORFOLK ISLAND.** Dawbin (1956) listed 113 shore-stations (and visited many of those disused sites) from which whales were captured by traditional methods in the 19th Century. Although the southern right whale was the preferred and initial quarry, humpback whale captures were noted from Cloudy Bay in 1841, Palliser Bay and Kaikoura in 1843, and the importance of the latter species increased as the century progressed. The tendency of humpback whales to migrate close to shore (and on occasions extremely so) was exploited by the Cook family who used steel nets to entangle whales at Whangamumu (Fig. 1) in the North Island from 1893-1910. The technique was unique, apart from net use in Japanese coastal whaling from the early 17th Century (Harrison Matthews, 1968). Nets were set between the shore and a nearby rock and most captures were made closest to shore in a channel <20m wide (Dawbin, 1956). Catches rarely exceeded 12 in a season (June-August) at this station which was among the most successful in New Zealand.

Traditional humpback whaling commenced at Norfolk Island in 1857 and continued, although with periods of interruption, until 1927 (Lewis-Hughes, 1992). Although operations were on a relatively small scale, the industry was an important income source for this isolated island, particularly as the victualling trade with American whaleships declined in the 60's during the Civil War. As was the practice in other areas using traditional methods, cows accompanied by calves were killed but the problem of a non-buoyant carcass was dealt with differently:

'In the early days whales were plentiful and were often killed close to the island, but as time went on the whaleboats were often forced to row or sail many miles out to sea to make a kill. The predominant species was the humpback which, unlike some others has an inclination to sink after it has been killed so, it was necessary for one of the boat's crew to tie or lash (some accounts say

sew) the monster's jaws shut to provide minimum drag when being towed and to reduce the chance of the animal filling with tons of water. Towing the whale tail first caused the flukes to extend at ninety degrees to its body creating great water resistance. If tail first towing was employed it was first necessary to sever the fluke muscles so that the flukes folded back along the whale's body once the tow commenced ... The whale of course was much larger than the boat and its great bulk did not improve the boat's sailing and pulling qualities.' (Lewis-Hughes, 1992). The methods employed at Norfolk Island were recorded on cine film in the late 1920's and a copy is held in the archives of the Queensland Museum.

As the 19th Century closed the earlier extensive pelagic whaling industry, based on sail, was virtually defunct. Small relic operations continued at Norfolk Island, Tonga and Twofold Bay as well as the net method at Whangamumu. This period of relative respite for humpback whales was to be brief and in the middle third of the following century, an unprecedented onslaught was unleashed.

#### MODERN WHALING

**NORWEGIAN EXPANSION SOUTHWARDS.** Progressive diminution of whale stocks in the North Atlantic at the close of the 19th Century resulted in increasing interest, particularly by Norwegian whalers, in the Southern Hemisphere. The first 'commercial' kill by modern methods was a humpback whale taken by A.A. Andresen in the Straits of Magellan on 31 December 1903 (Tønnessen & Johnsen, 1982). Activity initially centred on the rich grounds in the South West Atlantic, particularly at South Georgia (Fig. 2), and subsequently at lower latitude sites in South Africa and Western Australia. As the century progressed whaling extended to all aspects of the Southern Ocean. The extensive exploitation of humpback whales in the South West Atlantic was not initially repeated in other high latitude regions as shore-based and/or shore-related operations were not feasible. Whaling commenced in the Ross Sea (Fig. 2) in the summer of 1923-24 after the British government licensed Norwegians to operate in that region which included the Balleny Islands (Tønnessen & Johnsen, 1982). However, before further describing whaling in the Ross Sea consideration should be given to earlier Norwegian activity, involving modern methods, off the east coast of Australia. Dakin (1934) recorded the events in detail. Monson of Tønsberg formed

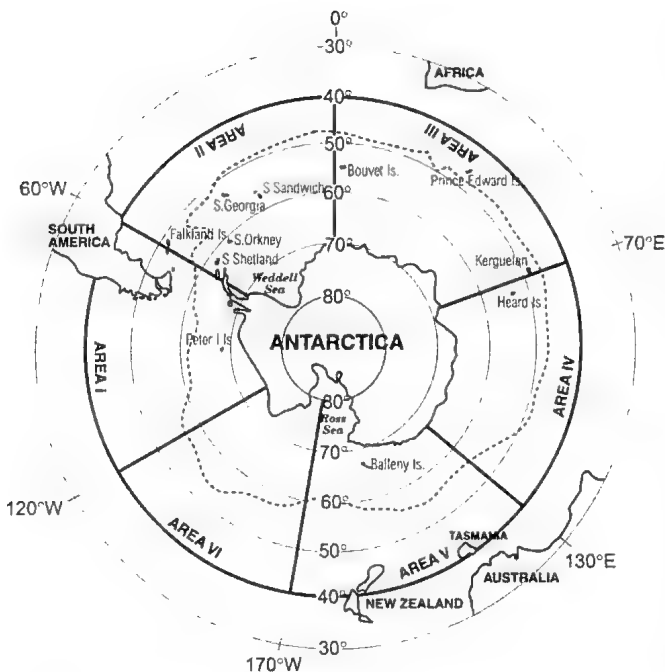


FIG. 2. Boundaries of six Southern Hemisphere whaling areas adopted in the 1930's.

the Australia Company in 1911 and sent the 8,000 ton factory ship *Loch Tay* with accompanying chasers to the east Australian coast in 1912. Operations commenced at Jervis Bay (Fig. 1) in September during the southern migration, and ceased at the end of November with an oil yield of only 3,000 barrels. Mitchell & Reeves (1983) considered that a humpback whale processed according to 19th Century methods yielded ~25 barrels. Assuming that 1912 methods were more efficient, it is likely that the catch at Jervis Bay was in the order of 100. The *Loch Tay* then proceeded to the Bluff in New Zealand where sperm whales were captured until May 1913 after which operations recommenced at Jervis Bay. The yield until October 1913 was 9,500 barrels, a catch possibly exceeding 300 although Dawbin & Falla (1949) estimated the catch at ~200-250. Numerous objections were received from local residents at Jervis Bay during the short 1912 season as well as from the authorities at the recently established Royal Australian Navy training college. They considered that whaling polluted local waters as well as causing offensive odours. Norwegian operations ceased at the end of the 1913 season for financial reasons rather than local objections and humpback whales migrating along the east Australian coast (apart

from small numbers taken at Twofold Bay) were spared from exploitation for a period of almost 40 years when operations commenced at the lower latitude sites of Byron Bay and Tangalooma (Fig. 1).

**NEW ZEALAND, NORFOLK ISLAND AND TONGA.** The Perano family dominated New Zealand whaling during the modern era. They captured their first humpback whale at Dieffenbach Point in the upper reaches of the Tory Channel adjacent to the Cook Strait (Fig. 1) in 1911 (Grady, 1982). Initial catches were modest. It was not until 1928 that more than 50 were captured in any season. The largest annual catch was 226 in 1960 prior to the end of the modern whaling era. In 1963 only 9 were captured. The total catch from the Cook Strait was 3,876 (Grady, 1982). The Peranos then directed their efforts towards sperm whales but ceased all whaling activity in 1964.

F.D. Ommanney visited the Perano's station in 1932 when the research ship *Discovery II* was refitting in Auckland. He noted that the plant was tiny and primitive by Antarctic standards and that Joe Perano knew nothing of Norwegian methods (Ommanney, 1933). He and his sons developed their hunting method in isolation and it was unique in many respects. Fast motor boats with a light bow-mounted harpoon gun were used and the harpoon line, also much lighter than that used by the Norwegians, was played from the stern of the chaser. The explosion of the grenade stunned but did not usually kill the whale. The boat was then brought alongside and the whale was inflated and then despatched by inserting into the upturned underside of the thorax a long lance with a hollow cast iron head filled with gelignite. It was then 'touched off' by an electric detonator. This method caused some fatalities to crew members. Ommanney considered the operation to be a modification of 19th Century traditional methods. In later years the Peranos developed more modern methods and their processing efficiency increased (Grady, 1982) but they still captured modest numbers based on a policy of voluntary restraint, which made their operation remarkable in the history of modern humpback whaling (Tønnessen & Johnsen, 1982). The Perano's method of cliff-top



sighting for approaching humpback whales was unique in the modern era, apart from similar methods (although from higher elevations) for sperm whales in the Azores (Clarke, 1954).

While in Auckland Ommanney also met W.H. Cook of Whangamumu net whaling fame. Nets had been abandoned in 1910 when a steam chaser was purchased. Captures, with males predominating, averaged 48 a year, with a record of 74 in 1927. Operations ceased permanently in 1931 (Ommanney, 1933).

In 1957 another station commenced at Great Barrier Island (Fig. 1) in the Hauraki Gulf (Dawbin, 1967) but initial catches were poor. Operations continued after 1959 under the auspices of the Barrier Whaling Company which had close commercial links with whaling operations at Byron Bay, on the east Australian coast, and Norfolk Island (Jones, 1980). Its success was brief and the station closed in 1962 after a total catch of 264 humpback whales (Dawbin, 1967 & 1997).

Humpback whaling, based on modern methods, re-commenced at Norfolk Island in 1948 under the control of the New Zealand owned South Seas Whaling and Sharking Company (Lewis-Hughes, 1992). That venture failed in 1949. In 1955 the Norfolk Island Whaling Company was formed as a subsidiary of the Byron Whaling Company and they subsequently merged to become the Norfolk Island and Byron Bay Whaling Company (Jones, 1980). A modern processing plant was installed at Cascade Bay where a rusting boiler remains today. In contradistinction to New Zealand operations, humpback whaling at Norfolk Island was subject to annual quotas (initially 150) set by Australian authorities after consultation with the International Whaling Commission (IWC). Varied timing strategies were employed at the Norfolk Island and Byron Bay stations. In 1956 operations commenced at Norfolk Island on 18 August (after the Byron Bay quota of 120 was filled) and ceased on 26 October (Jones, 1980). In 1957 operations commenced at Norfolk Island, transferred to Byron Bay in mid-season, and were completed at Norfolk Island. In 1958 the situation was reversed. In 1962 operations ceased after only 4 humpback whales were captured from a quota of 170. Total captures for 1956-62 were 824.

**TONGA.** Traditional humpback whaling modified from 19th Century American methods was conducted in Tonga by local inhabitants, including

those related to W.H. Cook of Whangamumu (W.H. Dawbin, pers. comm.), at least until 1978 (Paterson & Paterson, 1984), thus surpassing by almost half a century the other South West Pacific relic operations at Norfolk Island and Twofold Bay. As previously described at Norfolk Island, whale jaws were sewn together to aid towing, but the 'needle' was specially prepared humpback whale bone (J. Ovaleni, pers. comm.). Catches, described by Ruhen (1966), were small but Dawbin (1997) recorded a total of 87 from 1957-61 and a further 35 were reported from 1973-78 (IWC, 1980). The majority were cows accompanied by recently-born calves. Thus, for more than a century in the Tongan region, exploitation which ensured 'double mortality' was carried out firstly by Americans and subsequently by locals.

**EAST AUSTRALIAN COAST.** Following the Second World War, shore-stations based on modern methods were established at Tangalooma on Moreton Island and Byron Bay in 1952 and 1954 respectively. Whale Industries Pty Ltd, an Australian public company, controlled operations at Tangalooma although catching was dominated by Norwegian personnel. Jones (1980) provided an account of whaling activities, including detailed specifications of the chasers. Annual IWC quotas (increased to 810 in 1959) were readily filled in early years. However, the seasons lengthened as whales became scarce and Chittleborough (1965) noted progressive diminution in catch per unit effort (CPUE). The stations closed in 1962 after total captures of 7,423 from 1952-62. Paterson & Van Dyck (1988, 1995) reported additional, but incidental, catches of Bryde's whales *Balaenoptera edeni* and a single blue whale from Tangalooma and Byron Bay. Those limited captures illustrate the absolute reliance of the stations on adequate stocks of humpback whales.

**ANTARCTICA.** In 1923 the *Sir James Clark Ross* a modern factory ship entered the Ross Sea to search for abundant right whales reported on the discovery of this vast sea in 1841 (Dakin, 1934). The vessel was commanded by C.A. Larsen, a veteran Norwegian whaler, who died when the ship was near Victoria Land on 8 December 1924. Right whales were not found but blue whales were in abundance and perhaps the largest (31.8m) ever captured was taken at Discovery Inlet during that expedition (Tønnessen & Johnsen, 1982). It was soon appreciated that large numbers of whales congregated outside the

Ross Sea which had proved a difficult operational area due to variable ice and weather conditions. In 1929 whaling on a scale soon lamented by Harmer (1931) commenced beyond the pack ice north east of the Balleny Islands (Fig. 2). Captures of humpback whales in that region were in reality only in by-catch numbers at that time. Totals of 643 and 173 were reported in 1929-30 and 1930-31 respectively (Hjort et al., 1934). In the following decade, dominated by intense international pelagic whaling rivalry as well as the Great Depression and the outbreak of the Second World War, humpback whale catches in the region were small. Chittleborough (1965) noted 24 in 1938-39 and Omura (1953) reported an additional 201 in 1940-41.

The now familiar six Southern Hemisphere baleen whaling areas (Fig. 2) were designated following an international conference held in London in 1937. The regions of particular interest to this account are Area V and the western portion of Area VI. In an attempt to protect the interests of shore-stations and/or factory ships catching humpback whales along southern continental coasts as well as New Zealand, a ban on captures south of 40°S from 1 October 1938 to 30 September 1939 was implemented in a protocol (International Agreement for the Regulation of Whaling) agreed to in 1938 with the exception of Japan. This decision reflected increasing concern at the levels of exploitation of humpback whales at feeding and breeding locations as well as along coastal migration routes. In addition the capture of all baleen whale species was banned south of 40°S between the South Shetlands and the eastern Ross Sea (Fig. 2). These sanctuary provisions remained in force until 1955.

Following the Second World War, further attempts to regulate whaling and preserve stocks led to the formation of the IWC in 1946. The pre-war ban (relaxed temporarily in 1940-41) on humpback whale captures south of 40°S was continued until 1949-50 when a total Antarctic catch of 1,250 was permitted following Norwegian proposals (Tonnessen & Johnsen, 1982). Area V catches reported to the IWC from 1950-61 were 5,115 (Paterson & Paterson, 1984). Also included are the initially unreported 1955 catch of 1,097 by the *Olympic Challenger*. The saga of this pirate whaler owned by Aristotle Onassis and under the command of Wilhelm Reichert, which commenced operations off the South American coast in 1950, has been fully documented by Tonnessen & Johnsen (1982). It

operated in Area V in 1954-55 and, as elsewhere, humpback whales and other species were taken without restriction (mothers and calves included). Unfortunately, this episode was not the only instance of illegal Antarctic whaling in the closing stages of the modern era. Chittleborough (1965) considered that unreported captures of ~5,000 humpback whales occurred in Area V in 1960-62. He also noted that two correctly identified humpback whales marked with *Discovery* tags off Moreton Island and in the Cook Strait (Fig. 1) were reported as fin *Balaenoptera physalus* and sperm whales when subsequently captured in the feeding grounds. Given that mark recovery was low he considered it likely that these two recoveries indicated more numerous catches of 'mis-identified' whales. This masterly understatement of concern awaited 30 years for vindication which occurred after political upheaval in the former Soviet Union when Yablokov (1994) divulged preliminary information concerning illegal Russian Antarctic whaling activity in the late 1950's and 1960's. The enormity of this activity (in complete disregard for the convention and quotas of the IWC) has now been more fully documented. From 1959-62 humpback whale captures in Areas V and VI alone were 15,012. Whilst the earlier saga of the *Olympic Challenger* merited and received universal condemnation, it was in reality miniscule compared with the massive damage inflicted by a succession of Russian fleets acting in accord with deliberately secretive national policy. The *Slava* and the *Sovetskaya Ukraina* in a combined operation captured 11,605 humpback whales in 1959-60 (Mikhalev, 2000). They hunted primarily between 61°-66°S and 130°E-165°W and killed all whales seen, including mothers and calves. The *Yuri Dolgorukiy* captured a further 3,407 humpback whales in Areas V and VI from 1960-62 (Tormosov, 1995). Thereafter, the Russians abandoned those areas but captured a further 3,202 humpback whales principally from Areas II, III and IV between 1962-73.

## SUMMARY

At least 30,481 humpback whale captures have now been reported from Antarctic Areas V and VI, New Zealand, the east Australian coast, Norfolk Island and Tonga between 1950-62 with the Antarctic captures by the *Olympic Challenger* and the Russian fleets totalling 16,109 or 52.8% in less than four seasons. The IWC banned the capture of Southern Hemisphere humpback

whales in 1963. What has been the subsequent fate of those grossly depleted stocks? Machida (1974), who presumably had no specific knowledge of the illegal Russian activity, expressed great concern after the Japanese research vessel *Konan Maru No 16* saw only 7 humpback whales during a comprehensive survey of the Area V feeding grounds in March 1973. However, the east Australian humpback whale stock has demonstrated considerable resilience and long-term shore-based surveys at Point Lookout on North Stradbroke Island (Fig. 1) have demonstrated an annual rate of increase in excess of 10% (Bryden et al., 1990; Paterson et al., 1994, 2001). There is as yet no evidence of recovery in the New Zealand stock which had the particular disadvantage of prolonged 20th Century exploitation during its breeding, feeding and migration phases (Dawbin, 1997; Mikhalev, 2000). Dedicated surveys are considered to be presently unwarranted in New Zealand as there are no consistent reports of humpback whales from experienced casual observers such as Cook Strait ferry captains (C.S. Baker, pers. comm.).

Public opinion in the past 20 years has shifted considerably in favour of conservation. Commercial whaling is now prohibited in Australia (including its claimed Antarctic territory) and New Zealand as well as their respective exclusive economic zones. In 1994 the IWC declared the Southern Ocean a whale sanctuary, a measure not supported (or observed) by Japan. If these conservation attitudes are maintained and environmental factors remain constant, the near disaster which befell the humpback whale in the South West Pacific and adjacent Antarctic waters may ultimately be regarded as an aberration, albeit one which persisted for almost two centuries.

#### ACKNOWLEDGEMENTS

Noela Hilder is thanked for typing the manuscript.

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**SOUTHERN RIGHT WHALES, *EUBALAENA AUSTRALIS* (DESMOULINS, 1822), IN HERVEY BAY, QUEENSLAND.** *Memoirs of the Queensland Museum* 47(2): 430. 2001.:- Noad (2000) and Chilvers (2000) reported southern right whales in the Moreton and North Stradbroke Island regions of southern Queensland in 1998 and 1999 respectively. The lowest latitude sighting was 26°58'S at Flinders Reef.

At 9.30am on 27 September 2000 a southern right whale and calf were seen at 24°51'S, 153°08'E during a humpback whale sighting cruise in the Hervey Bay Marine Park. The mother/calf pair was moving slowly and milling at that location. They were observed and photographed from ~300m and were 'aloof' and 'shy' — characteristics commonly seen with humpback whale mothers and calves. The typical 'stubby' pectoral fin of the species was noted (Fig. 1A), as were the tail flukes (Fig. 1B), absence of a dorsal fin (Fig. 1C) and the 'bonnet' of the lightly-pigmented (presumably recently born) calf (Fig. 1D). Reports indicate that the pair was in the northern portion of Hervey Bay for at least two days.

This sighting extends the northern range of the species on the east Australian coast by 2° of latitude and supports the suggestion of Best (1993) that the range of formerly over-exploited mysticetes may expand as their populations

increase. The 'pre-whaling' range of southern right whales may have included Queensland waters but their near extinction in Australia by the early 1840s presumably precluded knowledge (at least by Europeans) of their occurrence at low latitudes. The above reports, in three consecutive years, may represent re-occupation of a former range and hopefully the species may become more frequent visitors to the Queensland coast, thus supporting the prediction of Noad (2000).

#### Acknowledgements

Members of the Hervey Bay whale watch fleet are thanked for their reports on the presence of the whales thus enabling this report.

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Jason Brigden, *Whalesong Cruises*, PO Box 620, Hervey Bay 4655, Australia; 20 March 2001.

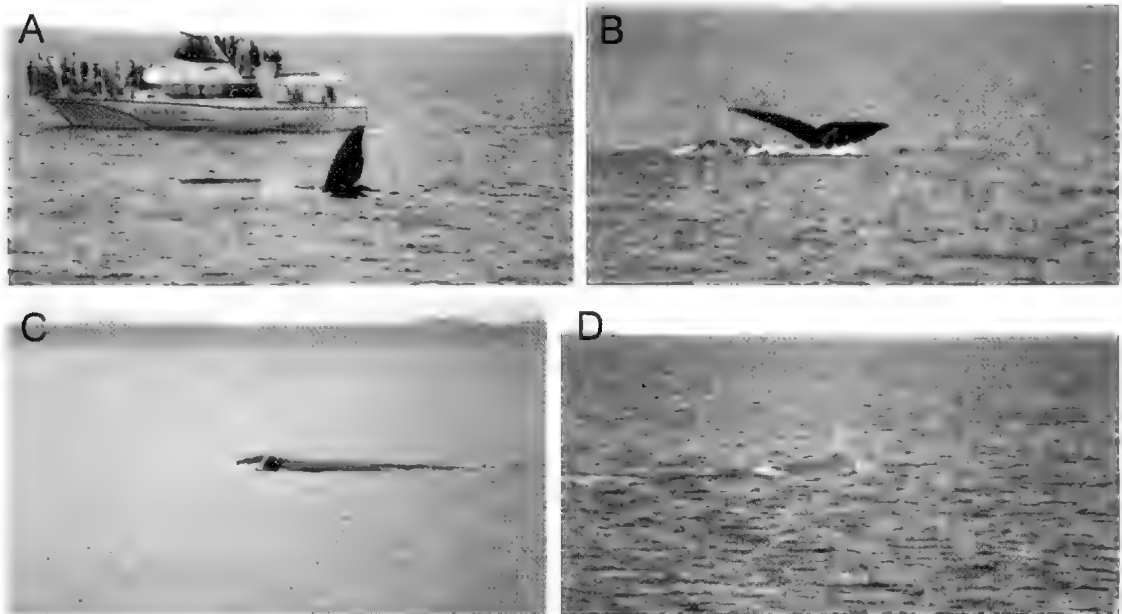


FIG. 1. Southern right whales in Hervey Bay, Queensland. A, pectoral fin of adult. B, fluke-up dive of adult. C, absence of a dorsal fin evident on adult. D, bonnet and generally light colouration of calf.

## ASPECTS OF HUMPBACK WHALE, *MEGAPTERA NOVAEANGLIAE*, CALF MORTALITY IN QUEENSLAND

H.A. JANETZKI AND R.A. PATERSON

Janetzki, H.A. and Paterson, R.A. 2001 12 31: Aspects of humpback whale, *Megaptera novaeangliae*, calf mortality in Queensland. *Memoirs of the Queensland Museum* 47(2): 431-435. Brisbane. ISSN 0079-8835.

The Queensland Museum has records of 19 humpback whale *Megaptera novaeangliae* calf mortalities. The cause of death in the majority was not determined. Three resulted from shark net drowning; two from shark attack and one from boat strike. Killer whale, *Orcinus orca*, attacks on calves are considered to be an uncommon cause of death in southern Queensland waters. □ *Humpback whale, Megaptera novaeangliae, calf mortality, Queensland.*

Heather A. Janetzki & Robert A. Paterson, *Queensland Museum, PO Box 3300, South Brisbane 4101, Australia; 16 August 2001.*

Humpback whale, *Megaptera novaeangliae*, calf specimens in the cetacean collection of the Queensland Museum and other recorded but not collected animals (Table 1) included 6 males, 5 females and 8 of unknown gender. All but two records post-date 1980. This is considered to have resulted from a greater capacity and interest in acquiring such specimens for museum collections, and recovery from low numbers following over-exploitation after the Second World War (Chittleborough, 1965).

### MIGRATION

**TEMPORAL AND SPATIAL FACTORS.** Most humpback whale calving on the east Australian coast is considered to occur in sheltered waters (18°-21°S) of the Great Barrier Reef during August and September (Simmons & Marsh, 1986; Paterson, 1991). In the small sample (Table 1), when accidental death such as boat strike and shark net drowning is excluded, 8 of the 15 deaths occurred in southern Queensland from late June to mid-August. One of us (RAP) has conducted a long-term study (Paterson et al., 1994) of the recovering east coast humpback whale stock from Point Lookout (27°26'S, 153°33'E) and Cape Moreton (27°02'S, 153°28'E). In 1999 as a continuation of that study both the northern and southern migration phases were observed. Most mother/calf pairs were seen at the end (October/November) of the southern migration (Fig. 1), a finding consistent with those of Chittleborough (1965) and Dawbin (1966, 1997). However, small numbers were seen in July during the northern migration indicating that occasional calving occurs at latitudes higher than Point Lookout. The mortality in July (Table 1), particularly in 1999, seems disproportionately

high but in the present state of knowledge it is impossible to attribute a specific cause, such as prematurity, to this. However, it is likely that calf mortalities in Queensland waters will increase as the population is increasing at ~10% per annum (Bryden et al., 1990; Paterson et al., 1994).

**PREDATION.** Two calves are considered to have died from shark attack (Paterson & Van Dyck, 1991; Paterson et al., 1993) although it is unknown if they had a constitutional condition which predisposed to predation. Protective gill nets set at surfing beaches along the Queensland coast since 1962 resulted in capture of 30,630 sharks until 1988 (Paterson, 1990) and the program is continuing. Whether the resultant regional captures of sharks have the potential to diminish attacks on humpback whale calves is debatable but will be a factor of interest in future studies. Killer whales, *Orcinus orca*, are also a natural predator of humpback and other baleen whales (Corkeron & Connor, 1999; Mead, 1963). During 931 viewing days from 1978-99 RAP observed 8,086 humpback whales passing Point Lookout or Cape Moreton and saw killer whales on only six occasions, including an attack on humpback whales on 10 October 1999 (Paterson & Paterson, 2001). Two attacks were photographically recorded by others on 19 October 1990 and 6 October 1998 and all three occurred within 3km of Point Lookout (Table 2). No remains washed ashore which is not surprising, given the combination of predator efficiency and prey non-buoyancy (Guinet et al., 2000). The attacks occurred in October when the majority of mother/calf pairs migrate through southern Queensland waters (Fig. 1). While opportunities exist for killer whales to attack humpback whales at other Queensland locations and at times not

TABLE 1. Queensland Museum records of humpback whale calf mortality.

Reg. No.	Date	Location	Length (m)/Sex	Cause of Death
-	1950s (winter?)	Point Lookout North Stradbroke I. (27°26'S, 153°33'E)	-	-
-	26.9.77	Surfers Paradise, Gold Coast (28°00'S, 153°26'E)	-	Drowned in shark net
QM JM7303	17.10.89	Moon Point, Fraser I. (24°14'S, 153°00'S)	4.2/♂	Shark attack
QM JM8658	19.7.91	Eagers Creek, Moreton I. (27°07'S, 153°27'E)	4.7/♀	Shark attack
-	3.8.92	Main Beach, Gold Coast (28°00'S, 153°26'E)	-	Drowned in shark net
QM JM12147	-	Airlie Beach (20°16'S, 148°43'E)	-	-
QM JM12148	26.11.97	Butchers Beach, via Bundaberg (24°48'S, 152°27'E)	5.6/♀	-
-	19.7.98	Eurong, Fraser I. (25°31'S, 153°07'E)	4.8/♂	-
QM JM13244	20.7.99	Dilli Village, Fraser I. (25°37'S, 153°05'E)	4.6/♀	-
QM JM13647	26.7.99	Dundubara, Fraser I. (25°10'S, 153°17'E)	3.6/♀	-
-	17.8.99	Cathedral Beach, Fraser I. (25°12'S, 153°16'E)	-	-
-	3.9.99	Grasree Beach, Mackay (21°16'S, 149°18'E)	4.0	Boat strike
-	26.10.99	Tangalooma, Moreton I. (27°11'S, 153°23'E)	5.8/♂	-
-	4.8.00	South Stradbroke I. (27°45'S, 153°27'E)	4.1/♂	-
-	26.6.01	North Stradbroke I. (27°33'S, 153°29'E)	4.6/♂	-
-	25.7.01	Kurrawa Beach, Gold Coast (28°02'S, 153°26'E)	4.7/♂	Drowned in shark net
QM JM14774	30.7.01	South Stradbroke I. (27°46'S, 153°26'E)	5.0/♀	-
-	13.8.01	Shoalwater Bay (22°20'S, 150°36'E)	4.5	-
-	13.8.01	Shoalwater Bay (22°36'S, 150°46'E)	~4.0	-

likely to be observed, it is likely that such attacks are an uncommon cause of humpback whale calf mortality in southern Queensland waters.

However, as the humpback whale population increases, numbers of ‘attendant’ killer whales may also increase. During aerial observations off Point Cloates (22°35’S, 113°40’E) on the Western Australian coast in 1952, when humpback whales

were then abundant, at least 130 killer whales were seen on 5 occasions (including an attack on a humpback whale group) between 17 August and 11 September (Chittleborough, 1953). On 24 September 1952 at least 150 killer whales were seen just to the north of Point Cloates in Exmouth Gulf (~22°S) where three humpback whales (including a calf) had been attacked, apparently

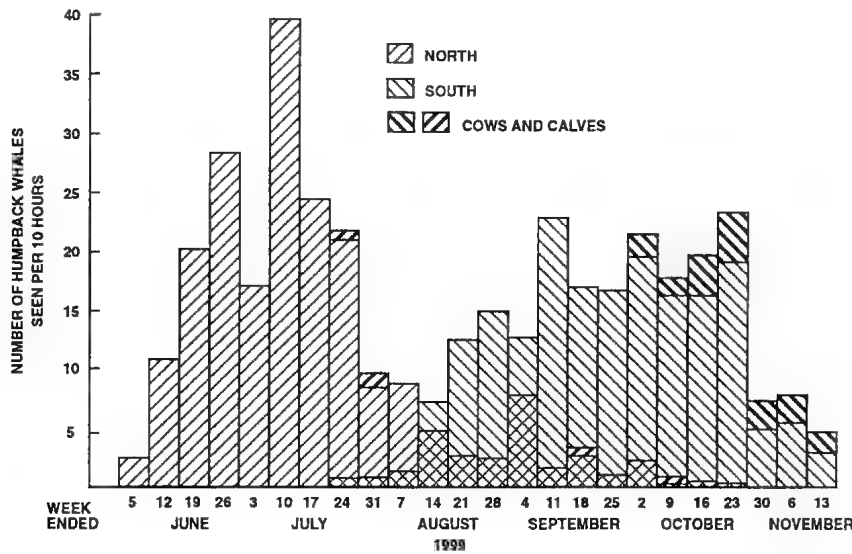


FIG. 1. Numbers of humpback whales seen per ten-hour period on a weekly basis at Point Lookout in 1999.



TABLE 2. Killer whales observed from Point Lookout (PL) and Cape Moreton (CM) during 1978-99.

Date	Location	Number	Direction (N/S)	Attacked humpback whales (Y/ N)
1.7.84	PL	~10	N	N
6.7.84	CM	~3	N	N
20.8.87	PL	>5	S	N
19.10.90	PL	?	S	Y
5.8.91	PL	~6	S	N
6.6.98	PL	3	N	N
6.10.98	PL	?	S	Y
10.10.99	PL	~10	S	Y

unsuccessfully, by killer whales in October 1951. Chittleborough (1953) considered Exmouth Gulf was a probable humpback whale nursery area given the high sighting rate of mothers and calves in that region during September and October.

**PARASITISM.** Although parasitism was not identified as a cause of mortality in these records the following information is considered important. The second largest calf QMJM12148, which was a 'late' (26 November) stranding, was the only one examined to exhibit external parasitism. Numerous barnacles (*Coronula diadema*) were recovered and occasional *Conchoderma auritum* were attached to the *C. diadema* (Fig. 2). The basal diameter of the *C. diadema* varied from 3.1-3.7cm, which is smaller than the majority of *C. diadema* recovered from an 8.1m yearling which stranded at Fraser Island on 3 July 1989 (Paterson & Van Dyck, 1991). The largest in that sample measured 4.6cm and Scarff (1986) recorded *C. diadema* of 5.0cm from adult humpback whales killed during whaling operations off Madagascar between mid-June and mid-August; by mid-September adult barnacles had disappeared and the whales were covered with free-swimming larval barnacles; by early October, small sessile adult barnacles were well attached.

QMJM12148, during its short life (presumably <6 months) spent in temperate waters of similar latitudes to those of Madagascar, had become infested with *C. diadema* which had already grown to a basal measurement exceeding 60% of those recorded from a yearling (Fraser Island) and adult (Madagascar) humpback whale(s).

#### DISCUSSION

Humpback whales frequent Queensland coastal waters during their annual migration and calf mortalities have been recorded from

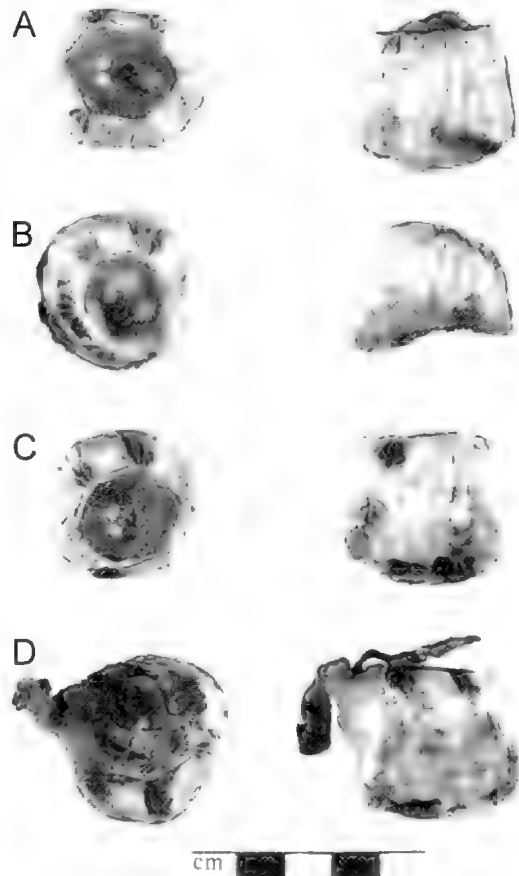


FIG. 2. *Coronula diadema* and *Conchoderma auritum* from a 5.6m humpback whale calf (QM JM12148), dorsal and lateral views. A-C, *C. diadema*. D, *C. auritum* attached to *C. diadema*. (Scale in cm).

June-November between latitudes 20°-28°S with an apparent disproportionate mortality during the northern migration in southern Queensland (Figs 1, 3 and Table 1). Pathological studies on fresh specimens may assist in elucidating the cause(s) of natural mortality in this population now recovering from over-exploitation.

Although the sample is small and presumably under-represents the incidence of calf mortality in Queensland waters, it is of note that human activity (protective shark net drownings and boat strike) contributed to the total. The Queensland Boating and Fisheries Patrol which administers the anti-shark program has been vigilant in recent years in early release of meshed humpback whales and has removed nets from strategic migration paths such as Point Lookout. Consequently, calf mortality from the anti-shark

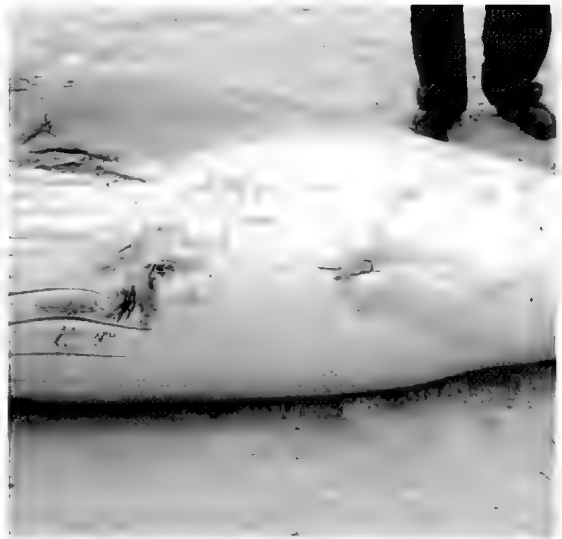


FIG. 3. New-born ♂ humpback whale calf stranded on North Stradbroke Island 26.6.01 showing attached umbilical cord and extruded penis. (Photos S. Benn)

program is likely to remain low. Long-term monitoring of humpback whale calf mortality in Queensland will assist in evaluating factors which may be deleterious to future stock recruitment.

#### ACKNOWLEDGEMENTS

Officers of the Queensland Environmental Protection Agency, particularly Steve Benn and Steve Winderlich, have assisted in the retrieval of specimens. Their efforts are much appreciated, as are those of Steve Van Dyck who recovered QMJM12148 under trying conditions.

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**A PRESUMED KILLER WHALE (*ORCINUS ORCA*) ATTACK ON HUMPBAC WHALES (*MEGAPTERA NOVAEANGLIAE*) AT POINT LOOKOUT, QUEENSLAND.** *Memoirs of the Queensland Museum* 47(2): 436. 2001. - Reports of fatal attacks by killer whales on humpback whales are uncommon (Flórez-González et al., 1994). This report describes a presumed killer whale attack with possible humpback whale calf mortality.

On 10 October 1999 during a survey of the southern humpback whale migration past Point Lookout (27°26'S, 153°33'E) on North Stradbroke Island (Fig. 1A) killer whales were first noted at 1128h in close association with a large (~5) disjointed group of humpback whales 300m south of Flat Rock (Fig. 1B). The position was at the extreme northern limit of visibility of the east facing 67m high shore position. Accordingly, it is not known when the encounter began. The events are best described as a mêlée with both species rapidly circling and changing course while blowing strongly similar to the ship-based observations of Flórez-González et al. (1994).

Humpback whale calves were not identified at that distance (~3km) but mother/calf pairs were identified at 0640 and 0657h on that day as well as on the preceding and following days. Calves were usually identified as they passed east of the observation position.

At 1228h the killer whales (~10) were concentrated in relatively deep water (Fig. 1A) ~800m east-northeast of Boat Rock (Fig. 1B) and appeared to be diving repeatedly and did not cease this activity until they dispersed at 1415h.

The original humpback whale group passed inshore of Boat Rock at 1228h, rounded its eastern aspect and returned

northwards. Three adults of the group then returned and remained in the vicinity of Boat Rock while two went south. On occasions, the three moved towards the killer whales and circled in the area until 1408h before passing out of sight in a northwest direction.

Such events have not been witnessed on any other of 931 days from 1978-99 when watching humpback whales from the same shore position. Most humpback whale calves seen from Point Lookout are paired with their mothers and are separate from other groups. Killer whales are known to attack baleen whale calves in low latitudes (Flórez-González et al., 1994; Corkeron & Connor, 1999). Although calves were not identified in the events described above, it is possible that a calf was already wounded before 1128h. The actions of the three adult whales may have been an attempt to 'assist' a dying calf, which was subsequently devoured in the area north of Boat Rock.

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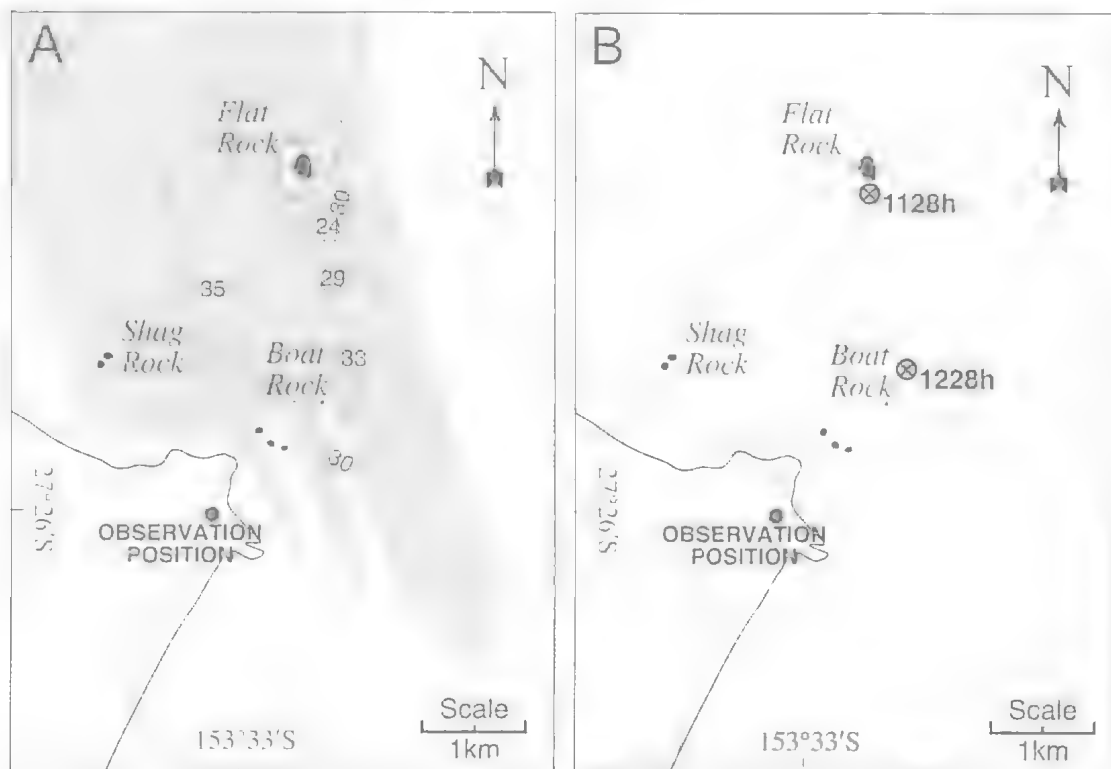


FIG. 1. Map of Point Lookout; A, course taken by southbound humpback whales (Paterson, 1991), relevant isobaths in metres; B, positions of initial and final stages of the killer whale attack observed on 10 Oct 1999.

## OBSERVATIONS OF A HYPO-PIGMENTED HUMPBACK WHALE, *MEGAPTERA NOVAEANGLIAE*, OFF EAST COAST AUSTRALIA: 1991- 2000

PAUL H. FORESTELL, DAVID A. PATON, PAUL HODDA AND GREGORY D. KAUFMAN

Forestell, P.H., Paton, D.A., Hodda, P. & Kaufman, G.D. 2001 12 31: Observations of a hypo-pigmented humpback whale, *Megaptera novaeangliae*, off east coast Australia: 1991-2000. *Memoirs of the Queensland Museum* 47(2): 437-450, Brisbane. ISSN 0079-8835.

In 1991 an apparently all-white humpback whale was observed and photographed from a shore-based observation platform in Byron Bay, NSW, Australia. The following year, the same animal (based on comparison of photographs of dorsal fin shape) was observed and extensively photographed in Hervey Bay, Queensland. Since then, more than 50 reports of white whale sightings have been obtained with reports in every year except 1997. The whale appears to be an albino and is the only documented occurrence of an all-white humpback whale. Sightings of this unusual animal provide important information on the migratory characteristics of humpback whales along the east coast of Australia. We investigated all known reports of a white whale from 1991-2000 and applied a scale of verifiability to each report. We plotted the location and time of each reliable sighting and summarised the range, rate of movement, social patterns and annual changes in migratory characteristics based on these reports. We present evidence that the white whale is now an adult male and relate its movements to what is known about male humpback whales from other studies. □ *Humpback whale, hypo-pigmented, white whale, Australia.*

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On 28 June, 1991 a humpback whale, *Megaptera novaeangliae*, exhibiting an unusual amount of white colouration was photographed near Byron Bay, NSW (Hodda, 1991) (Fig. 1). That was the only reported sighting of the uniquely marked whale that year. Subsequently, the presence of an apparently all-white humpback whale was reported at various locations along the east coast of Australia. We present a summary of sightings since 1991 and discuss the behaviour and significance of this unusual animal.

Humpback whales are regularly observed travelling along the east coast of Australia from June to November each year (Paterson & Paterson, 1989). Southern Hemisphere humpback whale stocks were reduced to <10% of pre-exploitation levels by commercial whalers between 1930-1960 (Allen, 1980). East Australian humpback whales were severely depleted by shore whaling stations at Tangalooma and Byron Bay operating between 1952-1962 (Paterson & Paterson, 1989; Paterson, 1991; Orams & Forestell, 1995). Chittleborough (1965) estimated population levels had dropped to <5% of pre-exploitation numbers when the International Whaling Commission in 1963 extended complete protection to Southern Hemisphere humpback

whales. Since then, studies conducted off the east coast of Australia have given evidence of recovery (Bryden et al., 1990; Paterson et al., 1994, 2001; Chaloupka et al., 1999). Bryden et al. (1990) and Paterson et al. (1994, 2001) have independently estimated the rate of recovery to be in excess of 10% per annum, based on annual counts from shore stations and aerial surveys over a 20 year period, during the annual migrations past North Stradbroke Island, Queensland. Chaloupka et al. (1999), analysed 10 years of re-sight histories of photographically-identified humpback whales in Hervey Bay, Qld, and concluded the east Australian Group V stock of humpback whales increased at a mean rate of 6.3% between 1988-1996.

Based on analysis of the recovery of marking darts (Dawbin, 1966), and reinforced by photographic documentation of the movement of one individually identified whale (Kaufman et al., 1990), it is generally believed east coast Australia humpback whales spend the austral summer feeding in Antarctic Area V (130°E-170°W). There, enormous supplies of the euphausiids upon which they feed allow them to store sufficient food reserves to last for most of the migration to and from lower latitudes, where

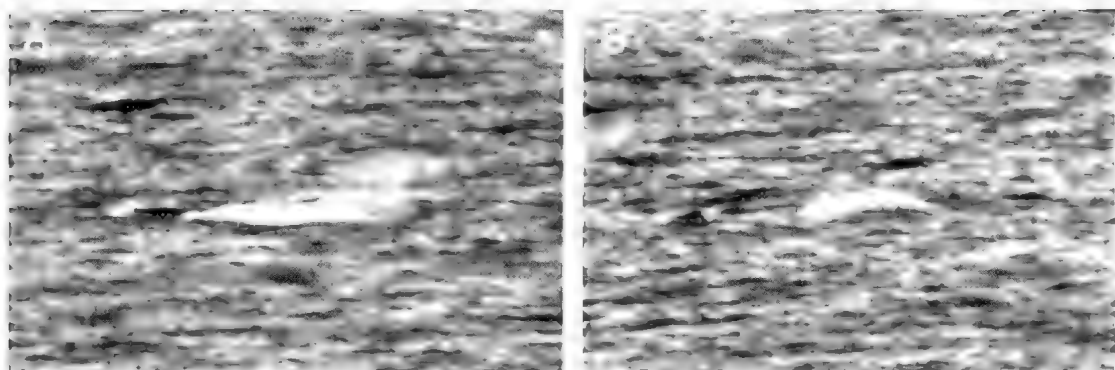


FIG. 1. First documented sighting of white whale, photographed 28 June, 1991 off Byron Bay, NSW. The whale is moving right to left, A, with remnants of the 'blow' seen near the dorsal fin; B, diving.

it is generally believed they do not regularly feed (Dawbin, 1956). Although humpback whales are found widely distributed throughout the Western South Pacific (Dawbin, 1964) the patterns of exchange between known wintering areas are still unclear. Garrigue et al. (2000) provide a summary of resights between east Australia, New Caledonia and New Zealand, and Baker (pers. comm.) has reported a match between east Australia and Tonga.

Analysis of repeated sightings of uniquely marked animals is an established method for obtaining information about population size, movement, group structure, site fidelity, reproductive rates and other life history patterns (Hain & Leatherwood, 1982; Würsig & Jefferson, 1990). Humpback whales are ideally suited to such studies, as they can be individually identified by variation in natural markings on the ventral surface of their tail flukes (Katona et al., 1979) and additionally by lateral body markings, particular in Southern Hemisphere stocks (Kaufman et al., 1987; Gill & Burton, 1995).

Confirmation of repeated sightings of identified humpback whales depends first upon obtaining high-quality photographs of the flukes and lateral body markings of animals and then careful documentation and comparison to ensure reliable determination of resight patterns (Hammond, 1990; Kaufman et al., 1993). Such efforts have been limited to a small number of skilled observers. Repeated sighting of an all white humpback whale since 1991 provided a further opportunity to study migratory patterns of Group V humpback whales as such a uniquely marked animal would be expected to have a high probability of being observed and identified by a wide range of observers.

Analysis of sightings of identified animals could clarify the extent of coast along which individual humpback whales may be observed during migration (Stone et al., 1990); minimum estimated rates of movement over long distances (Gabrielle et al., 1996); residency patterns in areas of known aggregation (Cerchio, 1998); and year-to-year differences in migratory timing (Baker et al., 1986; Krutzikowsky et al., 1991; Clapham et al., 1993). Additional information about social behaviours might be determined from data on pod size and composition and observations of behavioural displays of particular identified animals (Tyack & Whitehead, 1983). While recognising limits on the ability to generalise from the behaviour of one animal to the population as a whole, one might still uncover important information by tracking observations of uniquely-identified individuals over extended periods of time and space (Hain & Leatherwood, 1982). To our knowledge, the sighting history of the white whale described in this report constitutes the most detailed and long-term case study of a humpback whale's movement patterns.

## METHODS

**DATA-BASE.** A database of observations of a hypo-pigmented whale was developed to assess the reliability of the sightings; establish the range of times and locations over which the reports were made; examine behavioural details which might help determine the age and sex of the observed whale(s); and determine whether they were all of the same whale.

Reports of sightings of all-white humpback whales were identified through searches of newspapers, contacts with television stations and

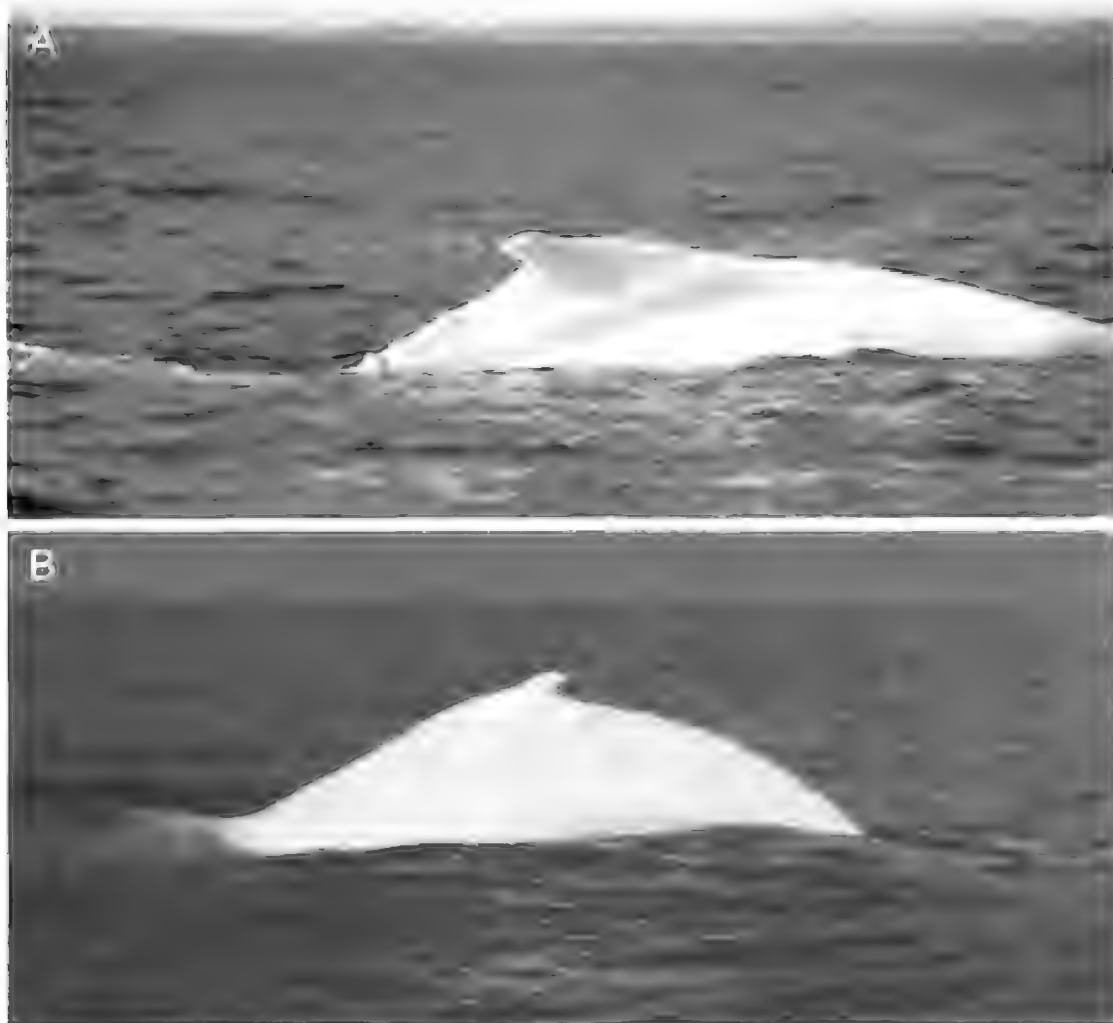


FIG. 2. A, right side of dorsal area, photographed 13 September, 1992 in Hervey Bay, Qld. B, left side of dorsal area, photographed 20 June, 2000 near Port Stephens, NSW.

interviews with researchers, government agencies and commercial boat operators. A difficulty of creating a database of reported observations obtained by a wide cross-section of the public is to verify the accuracy of reports. While anecdotal reports have been found useful in drawing conclusions about the status and behaviour of Group V humpback whales (Paterson & Paterson, 1984; Simmons & Marsh, 1986), it is probable that not all anecdotal reports are of equal reliability, and in the present case we attempted to differentiate between types of report. Reports were categorised as: 'Certain'- observations documented with movie, video, or still images; 'Likely'- first-hand accounts by

those qualified through training and experience to be considered experts in identification and observation of humpback whales (including field-based marine resource management agents, operators of commercial whale watch vessels, marine mammal scientists and laypersons specifically trained in observation of humpback whales); and 'Anecdotal'- all other reports.

For the purposes of our analysis, all Certain and Likely reports were considered reliable, while Anecdotal reports were excluded.

**ANALYSIS.** Once all reports were gathered and assessed, we compared photographs and videos across years to determine whether these sightings



were of the same animal. We then plotted the location of each reliable (Certain or Likely) sighting and determined the range and rate of movement for each year in which sufficient numbers of reports were obtained. We also assessed the information provided with each report to determine the nature of social behaviours exhibited by the whale, and hence its likely gender.

## RESULTS

Over 50 reports were gathered. When more than one report of a sighting was obtained at or near the same time (i.e., on the same day) only one report of the most reliable category was included. A summary of 35 unique sightings is summarised in Table 1 (Information on individual reports is provided in the Appendix). Twelve of the 35 observations were documented either by video or film, while an additional 13 were considered to be reliable reports by experts. Of the 10 sightings judged to be anecdotal, 4 occurred within one day of separate sightings of higher reliability in the same vicinity and the remaining 6 were without any corroborative support.

**COMPARISON OF IMAGES.** The sighting data indicate that only one all-white humpback whale has been observed off east Australia. Analysis of video and photographs from the 12 documented sightings of a white whale indicated the same animal was observed in each case. The whale has a distinctly curved dorsal fin, which is evident in each of the sightings (e.g., Fig. 2A shows the white whale observed in Hervey Bay, Qld on 13 September 1992; Fig. 2B in Port Stephens, NSW on 20 June, 2000). It is not possible to confirm whether the 13 'Likely' reports are of the same whale, since they are not supported by photographic evidence, however the sightings fit well within the patterns established by the 12 observations which were supported. These reports were generally consistent with what is known about migration of humpback whales along the east Australian coastline and occur in locations near the photographically documented sightings.

Photographs taken of the white whale have shown it as close as 20m at the surface and at ~150m from an aeroplane (Fig. 3). The entire dorsal surface of the whale is white, including the pectoral and tail fins. The whale has also been videotaped while breaching at a distance of ~100m. Observers reported viewing the ventral surface almost to the tail and, except for a clump

TABLE 1. Summary of observations of white whale for each sighting category within each year. \* In 1992 and 1993 a white whale was photographed by scores of individuals during the time (less than two full days) it was observed in the vicinity of Hervey Bay. However, only one 'Certain' report was included for each day on which the whale was photographed.

Year	Observations	Category	Days Observed	Places Observed
1991	1	Certain	1	1
	0	Likely	0	0
	0	Anecdotal	-	-
1992*	4	Certain	4	2
	5	Likely	5	5
	4	Anecdotal	-	-
1993*	2	Certain	2	2
	2	Likely	2	2
	3	Anecdotal	-	-
1994	1	Certain	1	1
	1	Likely	1	1
	2	Anecdotal	-	-
1995	2	Certain	2	2
	0	Likely	0	0
	1	Anecdotal	-	-
1996	0	Certain	0	0
	1	Likely	1	1
	0	Anecdotal	-	-
1997	0	Certain	0	0
	0	Likely	0	0
	0	Anecdotal	-	-
1998	1	Certain	1	1
	1	Likely	1	1
	0	Anecdotal	-	-
1999	0	Certain	0	0
	3	Likely	3	3
	0	Anecdotal	-	-
2000	1	Certain	1	1
	0	Likely	0	0
	0	Anecdotal	-	-
Totals	35		25	23

of barnacles attached to the ventral pleats, that surface was also completely white. The whale's tail flukes have been photographed and are completely white on both the ventral and dorsal surface (Fig. 4A, B). It appears the whale's skin is uniformly white over its entire body. It is also clear that the whiteness is due to natural colouration of the whale, rather than an artifact created by one of a variety of identified dermatoses due to bacteria, fungi, or ectoparasites (Migaki, 1987).

The most recent photograph (Fig. 2B) shows considerable yellow colouration along the whale's flanks. This is most probably due to the presence of an Antarctic diatom *Cocconeis ceticola*, which adheres to white areas of a humpback whale's body in a film-like covering (Burton, 1991). Bannister (1977) has suggested such colouration may indicate a whale which has recently moved from colder waters, which is consistent with the fact that the photograph was taken on 20 June, considered to be early in the northward migration (Dawbin, 1966).

**EXTENT AND RATE OF MOVEMENT.** Geographic locations of the 35 sightings of a white whale reported along the east Australian coast between 1991-2000 are shown in Fig. 5. The 25 reliable sightings clump into discrete areas: the Whitsundays Islands, Fraser Island, offshore Brisbane, Byron Bay, Port Stephens (just north of Sydney) and in the vicinity of Gabo Island near the NSW/Victoria border. This may reflect the high incidence of human activity in these areas, including both recreational tourism and commercial fishing, which increases the probability that the whale was observed when present. Another possibility is that the whale may have spent more time in some or all of these areas; or a combination of both possibilities may be at work.

The year 1992 was unusual in that 9 reliable sightings were obtained compared with 3 or fewer in other years. Using 1992 sighting data the whale's movement along the east Australia coast during the northward and southward migrations was plotted (Fig. 6), assuming a direct transit between known locations. The whale was first observed near Snowy River, Victoria, on the 9th of June — the next day it had moved ~100km east. Its most northerly reported location was in the Whitsundays on the 12th of August — a distance of ~2,345km in 64 days, (an average of 1.5km/hr, or 37km/day). The whale was also observed in the Whitsundays on the 13th of August. One month later (13th September) it was seen in Hervey Bay. Although next observed in Moreton Bay, the exact day is not certain. The last reliable sighting that year was near Eden, NSW on the 8th of October, a move of 2,153km from the Whitsundays in 59 days (1.5km/hr, or 36.5km/day). The final sighting of 1992 was approximately 200km from the first sighting 4 months earlier. The calculated rate of movement southward in 1992 was virtually identical to the northward movement (1.5km/hr).

The rate of migratory movement in 1992 was considerably slower than other estimates of humpback whale movements. Dawbin (1966) estimated migratory rate for humpback whales at 2.9km/hr over the duration of migration north and south, based on changes in the timing of peak catches at coastal whaling stations. Kaufman & Osmond (1987) reported short-term speeds of 8.7km/hr, based on theodolite observations of whales passing a headland on North Stradbroke Island (Moreton Bay, Qld). Using resights of photographically-identified individuals moving over more extended distances (e.g., between North Stradbroke Island and the Whitsunday Islands), Kaufman & Osmond (1987) estimated mean speed of migratory movement to be 3.1km/hr. Chittleborough (1953) noted that whales observed during aerial surveys along the coast of Western Australia averaged 8km/hr and ranging from 5-14km/hr. In Hawaii, Bauer (1986; cited in Gabriele et al., 1996) found that whales tracked with theodolite averaged 4.4km/hr, with a maximum of just over 11km/hr. Baker et al. (1985) used resights of 5 photographically-identified individuals to estimate an average of 1.9km/hr between Hawaii and Alaska, a rate more consistent with that shown by the white whale. In contrast, Gabrielle et al. (1996) reported a humpback whale photo-identified in southeast Alaska and 39 days later in Hawaii, requiring an average of 4.7km/h.

From these studies, variations in estimated rates of movement appear to reflect differences in scale. Observations of animals over extended distances have generally led to lower estimates than observations over short distances. Estimates based on photographic resights of animals more than two days apart may underestimate actual rate if it is not certain the whale was observed on its last day in one location or its first day in the next. Differences may also reflect significant changes in behavior at different points in the migration.

Brown & Corkeron (1995) argued that the migratory movement of humpback whales along the coast of Australia may be characterised by a behavioural continuum associated primarily with variations in breeding behaviour — including prospecting for mates, competition between males and possible mate-guarding. There is evidence of humpback whales engaged in feeding during the latter part of the migratory period, in the vicinity of Eden, NSW (Kaufman & Naessig, unpubl. data). Mate (1999) provided evidence that humpback whales, satellite-tagged



FIG. 3. Aerial view of white whale, accompanied by normally-coloured humpback whale, 14 September, 1992 near Hervey Bay.

in Hawaii, demonstrated highly variable individual patterns of movement at each stage of their annual cycle. Such patterns may be expected to result in a considerable variation in rates of movements within extended periods. A more detailed consideration of the white whale's movement reinforces such an expectation. Table 2 provides a breakdown of contiguous sightings of the white whale since it was first observed in 1991. Each entry reports the two successive

locations at which the whale was observed; whether the observation was during the northward or southward migration, or at the assumed terminus in the Whitsunday Islands; the year of the observation; the shortest straight-line distance between sightings; the number of days between sightings; and the calculated rate of movement. Rates range from a low of 0.38k/hr to a high of 6.33k/hr.

Overall, data on rate of the white whale's movement indicate a highly variable pattern, most likely associated with a range of activities over the ~4-month period travelling along the coast. These movements are consistent with Brown & Corkeron's (1995) conclusion 'that the migration of humpback whales is more than just a swim, and that the social influences on this species' migratory behaviour are subtle and complex'.

No observations of white whales were reported prior to 1991, or during 1997. Hodda (1991) noted that the white whale 'was too large to be a juvenile', although 'it did not appear to be fully grown', suggesting the whale was already between 3-5 years of age. The fact that the white whale was not observed as a calf or yearling prior to 1991, or during 1997 is of some interest, given its high visibility and the attention humpback

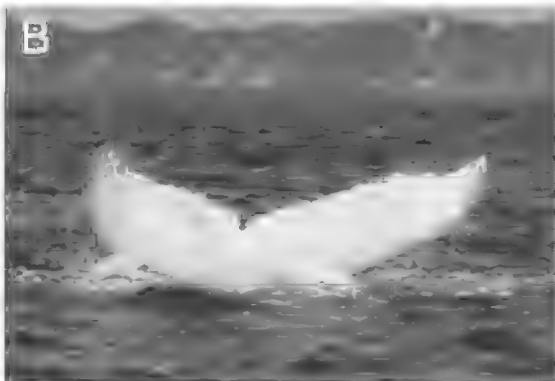
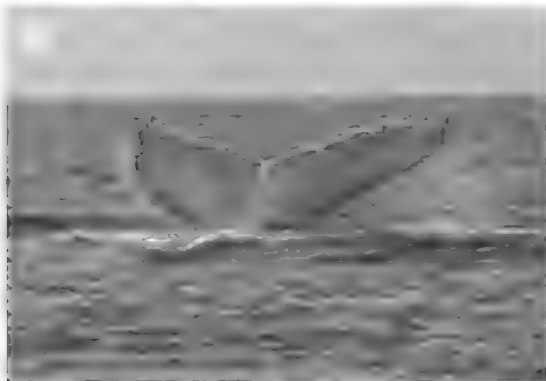


FIG. 4. Tail fluke; A, ventral surface; B, dorsal surface.

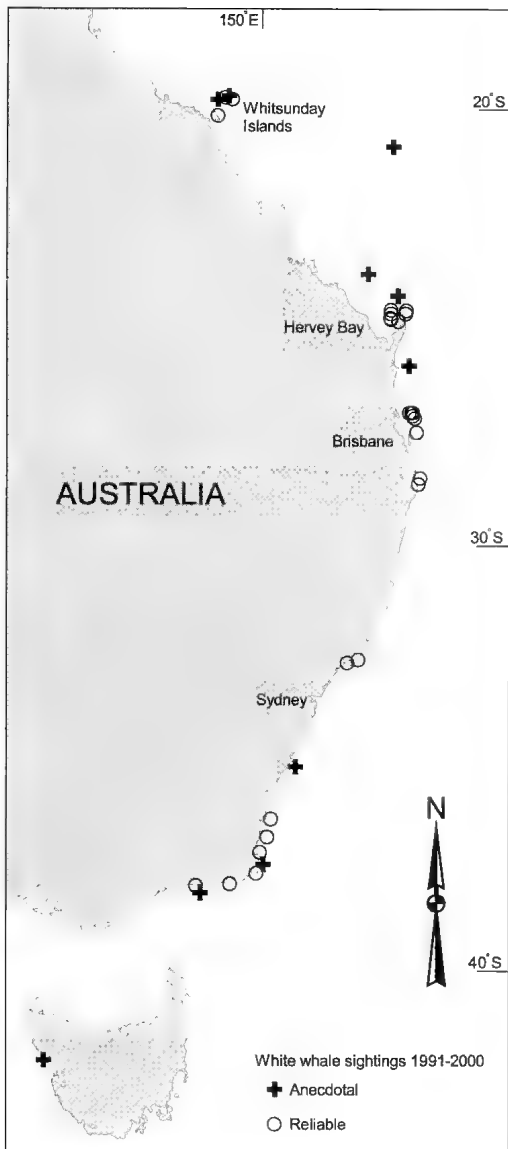


FIG. 5. Locations of reliable and anecdotal sightings of white whale from all reports from 1991-2000.

whales receive while migrating along the Australia coast. Movement of identified humpback whales between known wintering aggregations of the Southern Hemisphere has yet to be described in detail (Garrigue et al., 2000) and it is possible that in some years the white whale may have spent winter at a location other than east Australia.

**BEHAVIOURAL OBSERVATIONS.** The white whale is now at least 11 years old and based on an initial estimate of the animal's size and age (Hodda, 1991) it may now be 12-15 years of age.

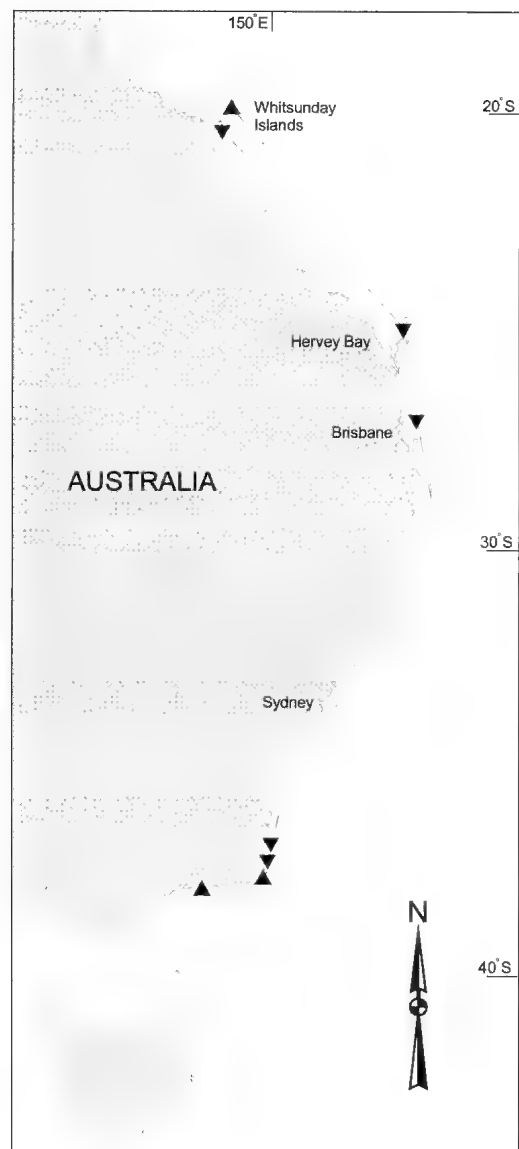


FIG. 6. Locations of reliable sightings: ▲, during northward migration, June – August, 1992; ▼, during southward migration, August – October, 1992.

Its behaviour over time has indicated it is a male, and perhaps a male that has recently reached reproductive maturity. In 1993 it was observed escorting a mother/calf pod — an indicator the animal is a male (Clapham, 2000). In 1998 during its visit to Hervey Bay it was heard singing (W. & T. Franklin, and M. Osmond, pers. comm.) — a more reliable indicator that it is a male (Glockner, 1983; Baker & Herman, 1984). In cases where pod size has been reliably reported, the white whale has been observed in pods of 2 in 40%,

TABLE 2. Distance and rate of movement between each set of contiguous reliable observations from 1991-2000.

Location	Direction	Dates	Year	Dist (Km)	Days	Km/hr
Snowy R. – Gabo I.	N	9 Jun – 10 Jun	1992	138	1	5.75
Byron Bay – Hervey Bay	N	16 Jul – 22 Jul	1995	422	6	2.0
Eden – Whitsundays	N	10 Jun – 12 Aug	1992	2207	63	1.46
Whitsunday Islands	N/A	12 Aug – 13 Aug	1992	15	1	0.63
Hervey Bay	S	13 Sep – 14 Sep	1992	10	1	0.42
Hervey Bay	S	29 Aug – 30 Aug	1993	15	1	0.63
Brisbane	S	1 Oct – 2 Oct	1999	43	1	1.79
Montague I. – Cape Everard	S	14 Oct – 15 Oct	1993	152	1	6.33
Tathra – Eden	S	6 Oct – 8 Oct	1992	42	2	0.88
Hervey Bay – Eden	S	14 Sep – 6 Oct	1992	1430	22	2.71
Hervey Bay – Brisbane	S	30 Aug – 29 Sep	1993	318	30	0.44
Whitsundays – Hervey Bay	S	13 Aug – 13 Sep	1992	674	31	0.91
Whitsundays – Hervey Bay	S	20 Jul – 2 Oct	1998	670	74	0.38

alone in 25% and with large surface active groups in 17%, including its most recent sighting near Port Stephens just north of Sydney in June 2000 (F. Future & S. Allen, pers. comm.). These observations are consistent with knowledge of migratory behaviour of adult male humpback whales (Dawbin, 1966; Clapham, 1994; Brown & Corkeron, 1995).

## DISCUSSION

**UNIQUENESS OF OBSERVATION.** To our knowledge, this is the first and only documented occurrence of a totally white humpback whale. Hain & Leatherwood (1982) and Fertl et al. (1999) summarised known accounts of anomalously white cetaceans listing no observations of humpback whales among the 22 species reported to have demonstrated albinism. Anecdotal accounts of white humpback whales exist (Baker, 1984; Weinrich, pers. comm.; Sharpe, pers. comm.) and recently a report was widely circulated of a 'mostly white' humpback whale in Niue, a small island nation in the South Pacific, east of Tonga and south of Samoa (Crowder, pers. comm.). However, such accounts generally suggest the animals were partly, rather than completely white. A disease known as Chediak-Higashi syndrome, which results in a 'bleaching' of normal skin colouration, has been reported in marine mammals (Matkin & Leatherwood, 1986). In such cases, however, some degree of shading is visible and is readily differentiated from true albinism on closer inspection.

We have observed whales in Hervey Bay that have been covered by barnacle scars or a white fungus-like covering that, from a distance, gave

the whale an appearance of primarily white with dark mottling. Group V whales are also known to have considerably less dark pigmentation overall than whales elsewhere (Kaufman et al., 1987). Northern Hemisphere humpback whales are generally quite dark overall, with perhaps 30% showing extensive white on the pectoral flipper and ventral fluke surfaces (Forestell, 1989; c.f. Fig. 7). Southern Hemisphere humpback whales demonstrate at least four types of colouration, with Type 1 showing the greatest extent of white (Fig. 8). Kaufman et al. (1993) found that ~20% of whales photo-identified off east Australia are Type 1 and another 20% are Type 2. It would not be unusual for lay observers to report an animal primarily observed from the ventral aspect, either above or below the surface, as a white whale, particularly if the observation is either brief or on only one occasion.

**IS THE WHITE WHALE AN ALBINO?** Whether the subject whale is a 'true' albino is

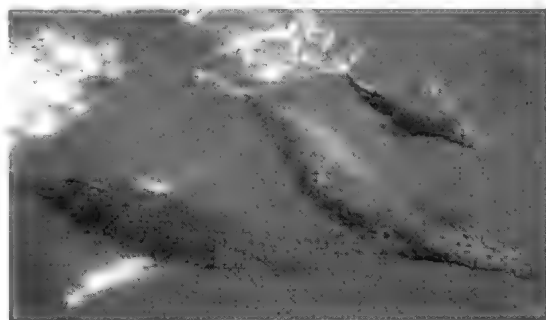


FIG. 7. Aerial view of mother, calf and escort humpback whale in Hawaii, showing colouration pattern typical of Northern Hemisphere animals.

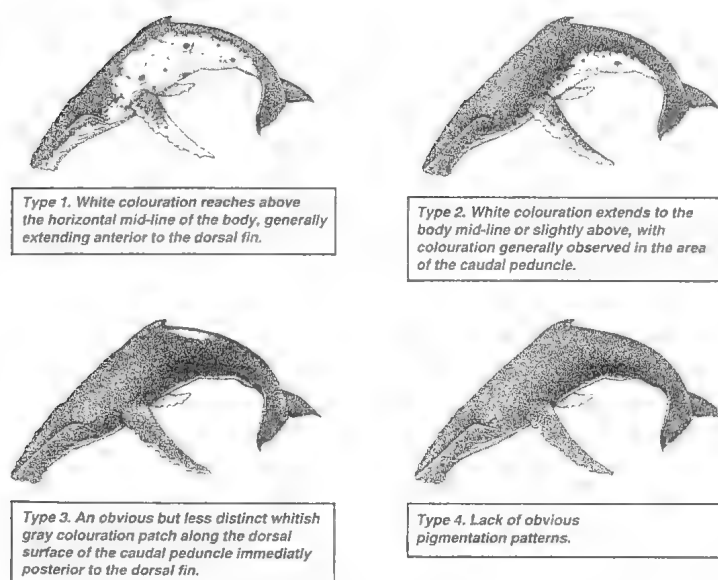


FIG. 8. Lateral body colouration patterns of humpback whales observed in the Southern Hemisphere, after Kaufman et al., 1987.

unclear. Albinism is a complex genetic defect in melanin production that results in partial or full hypo-pigmentation of the skin, hair and eyes, as well as abnormal development of oculoneural pathways (Oetting et al., 1996). The condition results when tyrosine is either not produced, or once produced is not properly metabolised into melanin. Albinism may involve any of a number of mutant alleles, resulting in a variety of phenotypes, ranging from partial to complete albinism. The mutant alleles may be autosomal recessive, autosomal dominant, or X-linked. Complete albinism, or tyrosinase-related oculocutaneous albinism (OCA1), is the result of recessive mutation in the structural locus for tyrosinase, which prevents melanin biosynthesis (Searle, 1990). OCA1 is generally associated with colourless skin, red irises and a variety of defects including mis-routing of the optic nerve and skin cancer. In contrast, ocular albinism (OA) affects only the eyes, but it also occurs in a number of varieties (Oetting et al., 1996). A number of complex diseases, such as Chediak-Higashi and Hermansky-Pudlak syndromes, include variations of albinism coupled with bleeding disorders and intestinal complications. Other pathological complications associated with hypo-pigmentation include lowered fertility, central nervous system defects and heightened susceptibility to infection (Hain & Leatherwood, 1982; Matkin & Leatherwood, 1986).

Analysis of photographs of the white whale raises three matters relevant to the question of albinism. A clear view of the eye is generally taken as the most direct means to determine whether albinism exists. There is no such view in any photograph to date although a distant image of the whale breaching (G. & M. Farrell, unpubl. photo) indicates faint pinkness in the eye region. An aerial image (Fig. 3), however, shows the region around the blowhole to be pink. While insufficient to diagnose albinism, observations so far are consistent with that conclusion.

A second point is related to the fact that humpback whales in the Southern Hemisphere normally show a great deal of white, compared with conspecifics of the Northern Hemisphere (Kaufman et al., 1987). When white areas are scarred by barnacles or by predatory strikes or other mishaps, the area scars black, at least initially and often permanently (Fig. 9). If the white whale was simply a 'normal' whale exhibiting an unusually large extent of what other normal whales display, then we should expect to find black marks anywhere that scars might have occurred. There is no such evidence. Barnacles can be observed on the tips of the flukes and in the ventral pleats, but there is no evidence of black scars in the 7 different years that photographs have been obtained. Based on the lack of pigment in scars, it is possible that the absence of colour in the white whale is the result of a mutant allele resulting in hypo-pigmentation similar to that associated with OCA.

A third feature is the presence of abnormal swelling and cyst-like protuberances in the head area. Photographs of the left side of the head from 1992 (Fig. 10A) and 1998 (Fig. 10B) both show an unusual deformity around the blowhole region, that is unlikely to be associated with skeletal malformation. In addition there are numerous small bumps caused by some type of sub-dermal abnormality. A frequent side effect of albinism is susceptibility to skin cancer in the absence of ultraviolet protection generally afforded by the presence of melanin (Oetting et al., 1996). If indeed this whale suffers from OCA1, then we might expect over time to see



FIG. 9. Tail fluke of normally-coloured humpback whale showing white ventral surface with black marks on scarred areas.

evidence of skin abnormality. Evidence to date is circumstantial but it appears that this animal is suffering from a skin disorder, which may be related to its hypo-pigmented condition. Taken together, we believe the indications of pink around the blowhole, the absence of dark pigmentation in marks and scars and the presence of skin abnormalities provide strong evidence that the white whale is a true albino.

IS THE WHITE WHALE A 'SPECIAL INTEREST' WHALE? OCA is assumed to be a recessive trait in all mammals, although molecular studies of albinism in animals other than humans are relatively rare. The frequency of OCA in humans is approximately 1 in 17,000 (King & Summers, 1988), while the frequency of OCA1 is approximately 1 in 40,000 (Oetting et al., 1996). No frequency estimates are available for other species. Since OCA is due to homozygosity for a recessive allele, and the condition is associated with a number of health risk factors, one might expect adult albino humpback whales to be rare. When isolated populations are reduced to relatively small numbers, however (as is the case with east Australia humpback whales), an abnormally high rate of occurrence of homozygosity in recessive alleles may result from inbreeding. When the condition is associated with a high probability of foetal or neonatal mortality, the rate of occurrence might not be obvious without genetic testing of the population. In the absence of genetic data, the most we can conclude is that to the degree the hypo-

pigmentation of the subject whale is genetically determined, the overall population seems not to be experiencing a genetic bottleneck.

Since its appearance in 1991 the white whale has generated a high level of media and public interest. To minimise possible harm to the whale from overly-curious humans the Queensland Government has made legal provision to treat it as a 'special interest' animal, and given regional wildlife managers the latitude to enact special provisions such as increased distance regulations (Jeffery, 1994). Treating the white whale as a 'special interest' animal, as unique and worthy of singular attention, is important for ensuring that particular animal is not harmed. One of the more striking revelations from study of the white whale is that, except for an amazing appearance, it seems no more special than the few thousand of its conspecifics that must 'adapt' to the presence of humans during their annual sojourn off Australia's east coast. The patterns we have described in the sightings of the white whale are comparable to those we have observed in normally coloured whales over 17 years. Resource managers have expressed concern that humpback whales may be subject to a cumulative impact of contact with human activity — from the Snowy River to Airlie Beach and back (Stevens & Page, 1995). It has become clear that, with significant growth in recovering whale populations in many areas of the world, the incidence of ship strikes has risen dramatically (Laist et al., 2001). Growing evidence of harmful effects of recreational boat traffic on marine mammals (Kruse, 1991; Constantine, 2001; Nowacek et al., 2001) amplifies proposals for greater use of 'precautionary' approaches to the regulation of human activities in the vicinity of marine mammals (Messe et al., 1999). The public fascination with the white whale may translate into coordinated efforts by all user groups to ensure the recovery of previously decimated marine mammal populations, including the humpback whales of east Australia, to their pre-exploitation levels (Hodda, 1996).

#### ACKNOWLEDGEMENTS

Thanks are due to many individuals who provided information on observations of a white whale. Specific sources of reports are noted in the Appendix. Appreciation is also expressed for assistance from the volunteers who have assisted the Pacific Whale Foundation and the Australian Whale Conservation Society in surveys of humpback whales during the period covered by this report. Richard King and Robert Pope



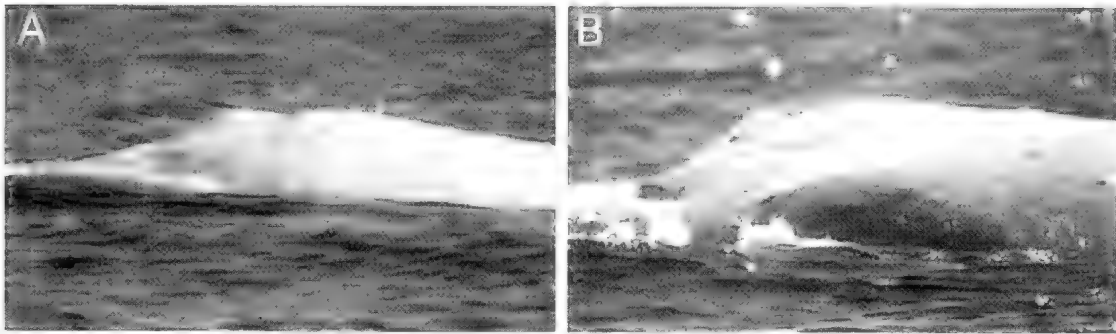


FIG. 10. White whale's head, left side, showing skin abnormalities; A, 1992; B, 1998.

provided important comments for the discussion on albinism. Photographs were provided by the Pacific Whale Foundation, except for Fig. 1 (Paul Hodda), Fig. 2B and Fig. 4A (Simon Allen). Figs 5 & 6 were prepared by Greg Luker of Southern Cross University. Southampton College of Long Island University provided the senior author release time from teaching to complete this report. We thank Dr Robert Paterson for his enthusiastic encouragement of our work.

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## APPENDIX

Details on each unique sighting of a white whale off east Australia, 1991 – 2000.

Date	Lat. Long. (°)	Location	Rel.	Pod Size	Activity	Dir.	Doc.	Comment
28/6/91	28.38, 153.38	Byron Bay	C	2 adults	Med Swim	N	Photo	P. Hodda
8/6/92	37.49, 148.37	Pt Ricardo, Vic.	A	2 Unk Sz	N/A	W	NA	Un-named surfer
9/6/92	37.49, 148.31	Snowy River, Vic	L	1 Ad, 1 Sub	N/A	?	NA	National Parks
10/6/92	37.21, 150.04	Green Cape, NSW	A	2 Adults	N/A	?	NA	Lay person
10/6/92	37.21, 149.55	Gabo Island, Vic	L	2 Unk Sz	N/A	?	NA	Lt Hse/Nat Prks
7/7/92	20.13, 149.00	Whitsundays, Qld	A	N/A	N/A	?	NA	Newspaper
8/7/92	19.47, 149.10	Bait Rf, Whitsundays, Qld	A	N/A	N/A	?	NA	Lay person
12/8/92	19.47, 149.10	Bait Rf, Whitsundays, Qld	C	1 Adult	Med Swim	?	Video	M. Wilson, Whitsunday Connection
13/8/92	20.13, 149.00	Hook Island, Qld	C	1 Adult	N/A	?	Video	Hamilton Island helijet, ref: H. Kobayash
13/9/92	24.55, 153.10	Hervey Bay, Qld	C	6 Adults	Resting	?	Photo	PWF, Many
14/9/92	24.55, 153.10	Hervey Bay, Qld	C	2 Adults	Active	?	Photo	PWF
?/10/92	27.00, 153.30	Moreton I, Qld	L	3 Unk Sz	Swim	S	NA	Lt Hse Kpr, Ref: R. Paterson
6/10/92	36.44, 150.00	Tathra, NSW	L	5 Unk Sz	N/A	?	NA	ComFshr, Ref: Roz Butt
8/10/92	37.05, 150.00	Eden, NSW	L	3 Unk Sz	N/A	?	NA	ComFshr, Ref: Roz Butt
21/6/93	35.08, 150.49	Jervis Bay, ACT	A	3 Unk Sz	N/A	?	NA	ComAbalone, Ref: Roz Butt
28/6/93	27.00, 153.30	Moreton I, Qld	L	2 Unk Sz	Swim	N	NA	LtHse, Ref: H. Kobayashi
8/8/93	20.55, 150.03	Kindermer Rf, Qld	A	7 Unk Sz	N/A	?	NA	Fishermen, Ref: H. Kobayashi
29/8/93	24.55, 153.10	Hervey Bay, Qld	C	1 Adult	Resting	?	Photo	Breach by G/M Farrell
30/8/93	24.55, 153.10	Hervey Bay, Qld	L	N/A	N/A	?	NA	DEH vessel
29/9/93	27.05, 153.30	Moreton I, Qld	C	2 Ad/1 Ca	N/A	?	Video	H. Kobayashi
24/12/93	41.49, 145.01	Granville Hbr, Tas	A	Mo/Ca	N/A	?	NA	Boat skipper
?/7/94	25.55, 153.25	Double I, Qld	A	N/A	N/A	?	NA	Newspaper
26/9/94	24.21, 153.09	Lady Musgrave I, Qld	A	N/A	N/A	?	NA	Fisherman
14/10/94	36.19, 150.15	Montague I, NSW	C	1 Subadult	Swim	S	Photo/Video	R. Constable, NSW/NPWS
15/10/94	37.48, 149.18	Cape Everard, Vic	L	N/A	N/A	?	NA	Trawler skipper
9/7/95	23.50, 152.28	Lady Elliott I, Qld	A	N/A	N/A	?	N/A	Un-named pilot, newspaper report
16/ 7/95	28.38, 153.38	Cape Byron, NSW	C	1 Adult	Slow Swim	N	Photo	R. Thompson, Skipper
22/7/95	24.41, 153.21	Fraser I, Qld	C	2 Adults	Slow Swim	N	Photo	Fshr/Tassy II, Lay person
?/7/96	24.41, 153.21	Fraser I, Qld	L	N/A	Slow Swim	N	NA	PWF/Soundings
20/7/98	19.47, 149.10	Bait Rf, Whitsundays, Qld	L	3 Adults	N/A	NA	NA	PWF/Soundings
2/10/98	24.55, 153.10	Hervey Bay, Qld	C	2 Adults	Singer	NA	Photo	PWF/Song rec by T&W Franklin
?/6/99	32.41, 152.15	Port Stephens, NSW	L	N/A	N/A	?	NA	W. Hamilton
1/10/99	27.00, 153.30	Moreton I, Qld	L	1 Adult	N/A	?	NA	Lt Hse Kpr, Ref: R. Paterson
2/10/99	27.25, 153.33	Nth Stradbroke I, Qld	L	1 Adult	N/A	S	NA	R. Paterson
20/6/00	32.41, 152.15	Port Stephens, NSW	C	5 Adults	Active	NA	Photo/Video	S. Allen/F. Future

# A MODEL FOR THE INTEGRATION OF MICROSATELLITE GENOTYPING WITH PHOTOGRAPHIC IDENTIFICATION OF HUMPBACK WHALES

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In this study we present a model for the integration of microsatellite genotyping with photographic identification of humpback whales, *Megaptera novaeangliae*, using samples from the east coast of Australia as a case study. A suite of 10 microsatellite markers was selected for this study, based on recommendations made by ANZECC and discussions with other research groups. Seven of the 10 markers were successfully used to genotype 12 sloughed skin samples from humpback whales on their northern migration along the east coast of Australia, resulting in 11 individual whales being identified. Two samples, collected from the same pod of whales, were found to be from one individual, as the genotypes of both samples were identical, while two further samples identified a pair of whales as a possible parent/offspring combination. In order to establish a worldwide database incorporating genetic and photographic identification of humpback whales, results must be standardised between research groups. To overcome potential technical difficulties of standardising results, we recommend that each research group sequence a reference sample or group of reference samples for each locus and that results are reported in repeat number rather than absolute PCR product size. □ *Microsatellite genotyping, humpback whale, Megaptera novaeangliae, photo identification.*

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Recent studies of humpback whales, *Megaptera novaeangliae*, have employed passive methods such as photographic identification of tail flukes and dorsal fins to examine site fidelity, basic social associations, migratory paths, population estimates and population growth (Isaacs & Dalton, 1992; Gill & Burke, 1999; Garrigue, 2001). Although much knowledge has been derived from photo-ID studies, the technique can be inconsistent and subjective, and susceptible to human error (Corkeron et al., 1999). Furthermore, young humpback whales can undergo extensive colour changes as they grow (Carlson & Mayo, 1990; Valsecchi & Amos, 1996), it is often difficult to approach animals due to behavioural responses and weather conditions, and individuals may lack distinguishing attributes necessary for unambiguous identification (Bain, 1990; Stern et al., 1990; Valsecchi & Amos, 1996).

As a result the Australian and New Zealand Environment and Conservation Council (ANZECC) recommended that genetic analyses be integrated with conventional research methods, such as photographic identification, to address remaining issues concerning humpback whale

populations. Microsatellite genotyping is a rapid, accurate and systematic technique, which can provide key insights into humpback whale ecology and evolution. While photo-ID does not lend itself readily to systematic profiling of individuals, it has the advantage of being a simple and obvious method of differentiating between individuals. A digital database incorporating both microsatellite genotyping and photo-ID of humpback whales would combine the advantages of each technique, providing information on population sizes, more detailed social associations, sex identification, mating strategies, stock structure, gene flow and parentage.

Southern Hemisphere humpback whales were classified into six stocks (Groups I-VI) by the International Whaling Commission (IWC) based on their aggregations in Antarctic summer feeding grounds. Genetic analysis of Group IV, V and VI stocks are of particular interest to Australian humpback whale research. Discovery tagging and acoustic analysis of Group IV and V stocks indicate that mixing of these populations is likely to occur (Chittleborough, 1965; Paterson, 1991), as is mixing of Group V and VI stocks (Valsecchi et al., 1997). Genetic differences

within and between these stocks remain unclear and movement patterns of individual whales across jurisdictional boundaries, within and between nations, need further investigation.

This study utilises 10 microsatellite markers to genetically 'fingerprint' 12 humpback whale sloughed skin samples collected during the Cape Byron Whale Research Project 2000. The microsatellite markers were selected as a standard set of genetic markers for humpback whale research in the Southern Hemisphere based on recommendations made by ANZECC (Corkeron et al., 1999) and discussion with other genetics laboratories in the Southern Hemisphere. Our aim was to establish a model for integrating microsatellite genotyping with photo-ID of humpback whales migrating along the east coast of Australia. Such information would provide a basis for establishment of a Southern Hemisphere humpback whale database.

#### METHODS

**SAMPLE COLLECTION.** During the Cape Byron Whale Research Project 2000, 91 sloughed skin samples were collected from humpback whales on their northern migration along the east coast of Australia. Where possible, accompanying photographs of the whale's tail fluke and dorsal fins were taken when the skin was collected. Byron Bay was selected for this study due to the close proximity of whales to the mainland, which allowed both land- and sea-based surveys to be conducted. Twelve skin samples were selected for microsatellite genotyping on the basis that each sample could be directly linked to an individual whale by being either the sole animal in a pod, or positively matched to a photo. DNA was extracted from approximately 1cm<sup>2</sup> of sloughed skin using the Tissue Protocol for the QIAamp DNA Mini Kit (Qiagen) according to the manufacturers instructions, with the exception that extracts were eluted with 2 × 100µl of buffer AE, instead of the 2 × 200µl recommended.

**LABORATORY ANALYSIS.** Ten humpback whale microsatellite loci were selected for microsatellite genotyping; EV14, EV21, EV37, EV94, EV96 & EV104 (Valsecchi & Amos, 1996), and GATA28, GATA53, GATA417 & TAA31 (Palsbøll et al., 1997a). The forward

primer of each locus was fluorescently labelled so that for each individual, PCR products could be combined for genotyping in two lanes of an automated sequencing gel without products overlapping in colour or expected size range (Table 1).

PCR amplifications were carried out separately for each individual/locus combination before PCR products were combined for gel separation. Locus EV94 was unable to be optimised and was not used for further analysis. PCR reaction mixtures contained: 1 × reaction buffer (Biotech), 0.1mM of each dNTP, 0.1µM of each of the forward and reverse primers, 0.55 units Taq (Biotech), 2.5mM MgCl<sub>2</sub>, 4µl of genomic DNA, and Milli-Q water to a total volume of 20µl. PCR reactions were performed on a PC960G thermal cycler (Corbett Research, Sydney) and run under the following conditions: 1 minute initial denaturation at 92°C, followed by 35 cycles of 10 seconds denaturation at 92°C, 30 seconds annealing at the optimised temperature (Table 1), and 1 minute extension at 75°C followed by a final extension step of 75°C for 5 minutes.

Genotyping of PCR products was conducted on an ABI Prism 310 genetic analyser (Applied Biosystems) using Genescan-500 TAMRA as an internal size standard. Results were displayed using *Genescan* software (Applied Biosystems). Genotypes were scored using *Genotyper* software (Applied Biosystems). Loci GATA417 and TAA31 were unable to be genotyped for the majority of samples and were not used for further analysis.

**DATA ANALYSIS.** In cases where two identical genotypes were found, the specific probability of identity (POI) for that exact genotype was calculated based on the POI formulae of Paetkau & Strobeck (1994). Due to the low sample size,

TABLE 1. PCR amplification conditions, number of alleles and expected and observed allele size ranges for the 10 microsatellite loci.

Locus	Dye label	Annealing temp. (°C)	Number of alleles	Expected size range (bp)	Observed size range (bp)
EV14	FAM	48	6	125-145	128-142
EV21	FAM	48	6	107-117	107-119
EV37	TET	50	12	190-228	190-218
EV94	TET	-	-	202-222	-
EV96	FAM	48	8	185-213	190-210
EV104	TET	48	3	143-153	141-145
GATA28	TET	48	5	147-191	144-178
GATA53	FAM	48	9	178-210	232-278
GATA417	HEX	50	-	193-293	-
TAA31	TET	48	-	85-121	-

we could not accurately determine allele frequencies and therefore the POI calculations lacked precision, however, the error was small.

## RESULTS

DNA from all 12 sloughed skin samples was amplified successfully at 7 loci (EV14, EV21, EV37, EV96, EV104, GATA28 and GATA53). Locus EV94 was unable to be optimised, while GATA417 and TAA31 were optimised successfully for PCR however did not amplify for the majority of samples. All 7 loci that successfully amplified were found to be polymorphic, exhibiting between 3 and 12 alleles (Table 1). The level of allelic diversity detected was similar to that of other studies, despite the comparatively small sample size (Valsecchi & Amos, 1996; Palsbøll et al., 1997a). The expected level of heterozygosity for each locus ranged between 0.55 and 0.98.

Alleles that were potentially unique to this study were detected at 5 loci, EV14, EV21, EV104, GATA28 and GATA53. All samples genotyped at locus GATA53 displayed a marked difference in the size range observed compared to that expected, with as much as a 66 base difference (Table 1). Four other loci displayed alleles outside their expected size ranges, but in each case this was only a difference of one repeat unit.

Samples B73 and B74 displayed identical genotypes at all 7 loci, while no two other samples shared the same genotype at more than 3 loci. These samples were collected in the vicinity of 2 whales migrating together. Samples B3 and B5 were the only other two samples (excluding B73 and B74) which had at least one allele corresponding at all 7 loci genotyped (Table 2).

These samples were also collected from within a pod of two whales migrating together.

Accompanying tail fluke photographs were obtained for 6 of the 12 skin samples, with each displaying a large variation in the degree of photo/camera angle, lighting and weather conditions. Photo-IDs were matched alongside their respective microsatellite genotypes for comparative purposes (Fig. 1).

## DISCUSSION

For over two decades attempts have been made to photographically identify individual humpback whales around the world. Recent advances in genetic techniques now provide a more informative form of individual identification. Microsatellite genotyping can provide information on contemporary population structure, gene flow, abundances, relatedness and genetic diversity (e.g. McRae & Kovacs, 1994; Richard et al., 1996; Call et al., 1998; Palsbøll et al., 1997b), enhancing the information available from photo-ID research.

In this study, 11 individuals were positively identified using a suite of 7 hypervariable microsatellite loci. The level of variation detected could distinguish all but 2 of the 12 samples from as little as 1 locus (e.g. Fig. 1, GATA53), illustrating the accuracy with which this method can identify individual humpback whales. The two samples (B73 and B74) that could not be distinguished are most likely to be from one whale sampled twice. The specific probability of identity of the exact genotype shared by these two samples is  $8.189 \times 10^{-17}$ ; calculated from the frequency of alleles observed, which is an imprecise estimate of the frequency of alleles in

TABLE 2. Genotypes of humpback whale sloughed skin samples for 7 microsatellite loci.

Locus sample	EV14	EV21	EV37	EV96	EV104	GATA28	GATA53
A7	128/ 130	113/ 115	192/ 194	198/ 202	143/ 143	144/ 152	232/ 244
A8	130/ 132	109/ 109	196/ 204	196/ 202	143/ 145	144/ 144	248/ 256
B3	130/ 132	107/ 109	206/ 218	196/ 200	143/ 145	144/ 144	232/ 260
B5	130/ 136	109/ 109	190/ 206	200/ 202	143/ 143	144/ 148	232/ 256
B54	130/ 132	107/ 109	202/ 208	200/ 204	141/ 145	148/ 176	236/ 248
B73	130/ 136	113/ 115	198/ 210	196/ 206	143/ 143	152/ 180	252/ 252
B74	130/ 136	113/ 115	198/ 210	196/ 206	143/ 143	152/ 180	252/ 252
B78	132/ 136	119/ 119	210/ 218	194/ 202	143/ 143	-	-
B92	132/ 132	109/ 111	190/ 192	202/ 202	143/ 145	144/ 152	256/ 264
B97	138/ 142	107/ 115	192/ 194	196/ 196	143/ 143	144/ 144	232/ 248
C2	130/ 130	109/ 109	194/ 206	198/ 200	143/ 143	144/ 152	248/ 252
E10	130/ 130	107/ 115	196/ 212	204/ 210	143/ 143	144/ 144	232/ 276

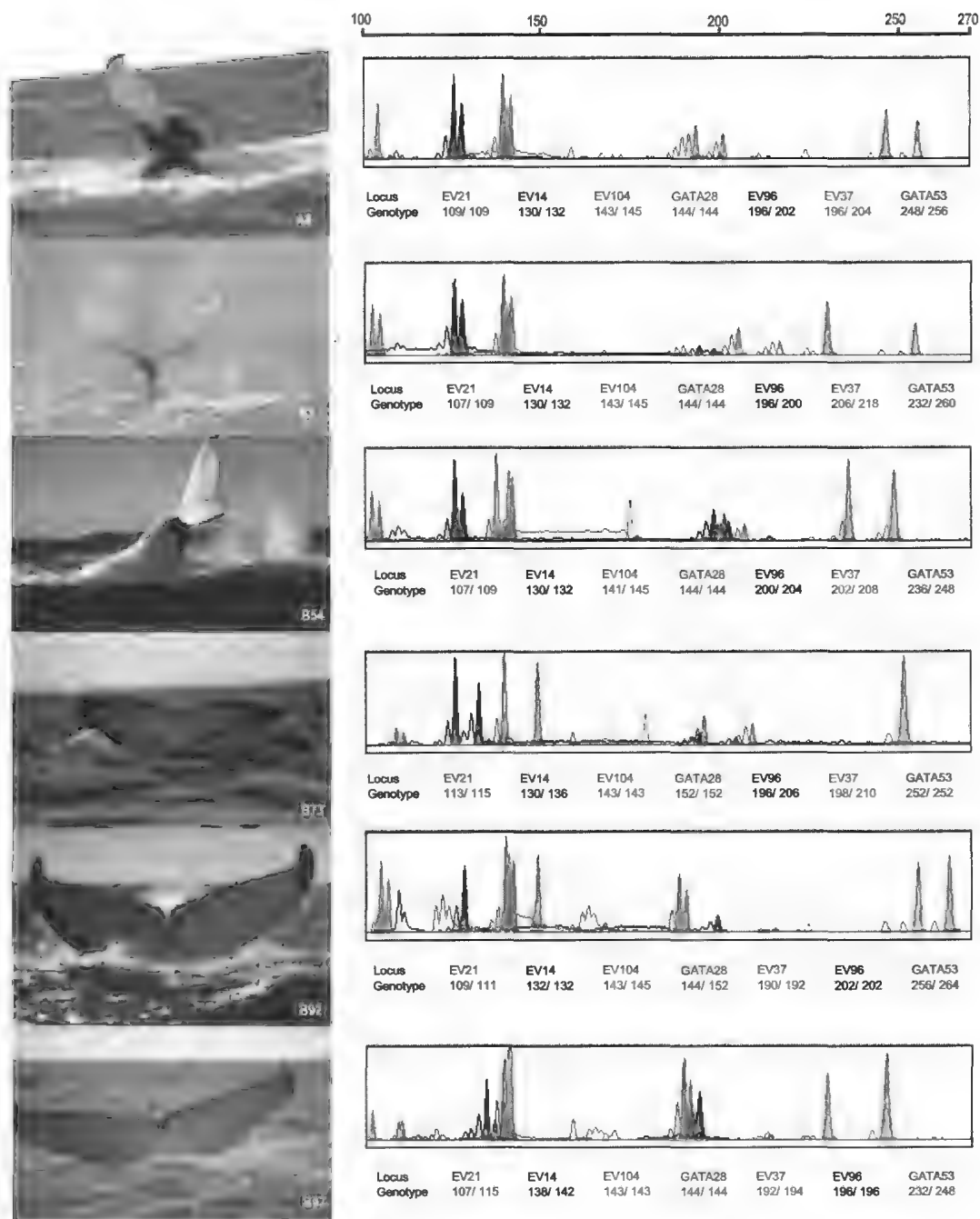


FIG 1. Individual identifications of humpback whales migrating north past Byron Bay, using photographic identification and microsatellite genotyping. Genotypes are shown for 7 microsatellite loci.

the population, and is therefore only an estimate of the exact probability of identity. Considering the extremely low probability of these two sample genotypes being identical by chance

alone and the fact that they were obtained from the one pod of whales, it is likely that these two samples came from the same whale.

This result highlights a potential source of error when using sloughed skin for microsatellite genotyping purposes. Skin can remain in the water column for up to 20 minutes after being dislodged (Corkeron et al., 1999), therefore samples collected from pods containing several whales are less reliable for microsatellite genotyping purposes. Valsecchi et al. (1998) found biopsy darting to be the most efficient method for matching samples to individuals, however this technique still cannot guarantee a match between a microsatellite genotype and photo-ID.

Samples B3 and B5 were found to share at least one allele in common at all 7 loci genotyped, suggesting that these two individuals may be related. Other studies have shown that associations between humpback whales tend to be non-related (except in the case of mother-calf pairs) and transient, with few pairs being associated through time (Falcone et al., unpubl. data). Valsecchi et al. (in press) concluded that migrating humpback whales did not select their travelling companions based upon relatedness at any stage of the migration. Results of the present study, however, suggest that humpback whales may migrate as family units, as both individuals sampled were adults and not a mother-calf pair. Unfortunately, due to the small sample size and the limited number of loci genotyped, the inference of familial relationships based on allele frequencies is not strong. In order to definitively determine potential relationship between individuals, as many as 17 loci may need to be genotyped to minimise the chance of random matches (Palsbøll, 1999).

For data to be shared effectively between research groups there are potential technical errors that need to be addressed, including: non-templated addition of a single adenine base by *Taq* DNA polymerase during PCR (Brownstein et al., 1996; Magnuson et al., 1996); allelic dropout resulting from poor quality template DNA due to degraded or low quantity DNA (Jarne & Lagoda, 1996); null or non-amplifying alleles (Brookfield, 1996; Jarne & Lagoda, 1996); calibrating PCR product size scoring across hardware; and confirmation of amplification of the correct locus.

Addition of an adenine base during PCR (+A) can cause problems in allele scoring during genotyping (Magnuson et al., 1996). The frequency of +A addition can vary within and between loci, as well as within and between different gel runs, and can be affected by different

DNA polymerases (Brownstein et al., 1996; Magnuson et al., 1996). Several procedures can be used to overcome this problem. 1) A reference sample or group of reference samples should be sequenced for each locus and always included in every PCR and gel. The correct product size can then be determined and correct binning boundaries set. 2) Alleles should be recorded as numbers of repeats rather than absolute PCR product size. 3) Different combinations of primer modification and DNA polymerase can be used to either induce 100% +A addition or reduce +A addition to 0%, so that results can be standardised accordingly.

When using small quantities of poor quality or degraded DNA, often only one allele of a heterozygous individual is detected (Taberlet & Luikart, 1999). This type of error, called allelic dropout, creates an artificial excess of homozygotes, possibly resulting in departures from Hardy-Weinberg equilibrium. A similar problem is the amplification of null alleles, which occurs when mismatches in the priming site of one allele cause the failure of that allele to be amplified, again causing an excess of homozygotes. Allelic dropout and null alleles can be differentiated as allelic dropout is associated with low quality DNA and therefore can be detected across loci within an individual, whereas null alleles are associated with a specific locus and can be detected across individuals within a locus. Another potential problem associated with null alleles, is the use of primers designed for one species to amplify a homologous locus in another species. In such instances more species specific primers may need to be designed. If reference samples for a locus have been sequenced and aligned, conserved sequence blocks can be identified so that new primers can be designed for those regions, reducing the risk of null alleles. By recording results as repeat numbers rather than PCR product size, allele sizes can be directly compared between different primer pairs for the same locus.

The use of different hardware for genotyping can result in identical samples being scored as different sizes. Calibration of hardware within and between research groups can be achieved by sequencing a reference individual or a group of reference individuals for each locus, and always including these reference samples in every PCR and gel. Furthermore, allele scoring can be standardised by recording data as repeat number rather than PCR product size. A number of loci in this study exhibited what seemed to be extensions



to their known size range, but these may have been the result of incorrect scoring or binning of genotypes, or non-calibration of hardware between laboratories. Hardware calibration and standardised definition of binning boundaries are therefore essential to eliminate potential scoring errors.

When comparing results between research groups it is vital to ensure that the same locus has been amplified in all instances. Sequencing of a reference individual or group of reference individuals will establish whether or not the same locus is being amplified. While such an event may seem unlikely, it did occur in this study. For locus GATA53 we used the primers published in Palsbøll et al. (1997a). Our results showed that the size range differed from the expected by 66 bases. Investigation revealed that one of the published primers was unlikely to be the primer used in that study. Furthermore, when we compared the two primer pair sets on the same individuals, not only did the allele sizes differ, but the relative allele size ranges within individuals also differed. Despite the change in only one primer, it appeared that a different microsatellite locus had been amplified. The only method to test this hypothesis would be to sequence the products for both sets of primers.

This study presents a model for the integration of microsatellite genotyping with photographic identification of humpback whales, using samples from the east coast of Australia as a case study. A standardised digital genetic database would greatly benefit research of humpback whale populations through sharing of results worldwide among research groups and be of immense value for conservation and management purposes. Integration of such a database with current photo-ID databases would enhance the value of each by incorporating the accuracy of microsatellite genotyping with the wealth of photo-ID data available.

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**MIGRATING MOLECULES – GENETIC IDENTITY AND DIFFERENCE AMONG HUMPBACK WHALES, WORLD-WIDE.** (ABSTRACT) Over the last decade, molecular genetic investigations of skin biopsy samples collected from humpback whales (*Megaptera novaeangliae*) have provided a remarkable description of the social relationships, migratory habits and historical demography of this cosmopolitan species. In many cases, genetic markers have been used to test and extend previous hypotheses based on long-term studies of naturally marked individuals. In other cases, they have provided novel insights into the evolutionary dynamics and history of populations. Here I first review basic characteristics of the markers used for these studies, including sequence variation in mitochondrial (mt) DNA control region, length differences in alleles of nuclear microsatellite loci (or Short Tandem Repeats), and sequence variation of introns and exons of functional nuclear genes. I then review or introduce selected examples of the applications of these marking from published or ongoing studies in my laboratory, some of which will be presented in greater detail by others at *Humpback Whale Conference 2000*. These include: the identification of individuals in populations; analysis of kinship among social groups; descriptions of maternally directed fidelity to migratory destinations; evidence for sex-biased gene flow between wintering grounds; estimation of long-term gene flow among oceans; and detecting humpback whale products for sale on commercial markets in Japan and Korea.

**WORLD-WIDE DISTRIBUTION OF NUCLEAR GENETIC MARKERS IN HUMPBACK WHALES.** (ABSTRACT) We compare allelic variation in a nuclear actin intron with that observed in three microsatellite loci among oceanic populations of humpback whales (*Megaptera novaeangliae*). The presence of two highly divergent actin allele lineages was confirmed in the three oceanic populations (Palumbi & Baker, 1994). The distribution of the two lineages is consistent with divergence of each through historic isolation and the subsequent dispersion of both lineages during one or more periods of trans-oceanic gene flow. Sequencing and SSCP analysis resolved the two divergent lineages further into eight alleles. Of the four common alleles, two were globally distributed, one was common only to North Pacific and Southern Indo-Pacific populations, and one was unique to the North Atlantic. Of the rare alleles, southern Indo-Pacific populations shared one, one occurred in a subset of North Pacific and southern Indo-Pacific populations, and

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two were population specific. In comparison to the intron data, the microsatellite loci showed reduced levels of population differentiation and the absence of unique oceanic alleles, perhaps as a result of size homoplasy. In contrast to the distribution of mtDNA lineages, which suggest a more recent connection between the North Atlantic and southern Indo-Pacific oceans, the distribution of nuclear alleles suggests a more recent historic connection, or male-mediated gene flow, between the southern Indo-Pacific and North Pacific oceans.

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# GENETIC CHARACTERISATION OF THE COLOMBIAN PACIFIC COAST HUMPBACK WHALE POPULATION USING RAPD AND MITOCHONDRIAL DNA SEQUENCES

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Caballero, S., Hamilton, H., Jaramillo, C., Capella, J., Flórez-González, L., Olavarria, C., Rosenbaum, H., Guhl, F. & Baker, C.S. 2001 12 31: Genetic characterisation of the Colombian Pacific Coast humpback whale population using RAPD and mitochondrial DNA sequences. *Memoirs of the Queensland Museum* 47(2): 459-464. Brisbane. ISSN 0079-8835.

Two genetic techniques were used to characterise the humpback whale population that overwinters annually off the Pacific Coast of Colombia. A preliminary study applied molecular techniques to an initial set of 32 biopsied or sloughed skin samples. Randomly Amplified Polymorphic DNA (RAPD) was used to provide an estimate of genetic variability and intra-population structure. Diversity of RAPD banding patterns suggest substantial genetic variability among sampled individuals. A parsimony tree was constructed using presence/absence of RAPD bands as characters, revealing three distinct groups: one of closely related individuals separate from two distinct clades within which relationships were unresolved. Mitochondrial DNA sequences for a consensus fragment 283 base pair in length of the rapidly evolving mitochondrial control region were then generated for the 32 samples and an additional 48 skin samples obtained from further fieldwork. An extensive comparative analysis was made with both published and unpublished control region sequences from humpback whales previously sampled in Colombia (n=64) and other regions in the Southern hemisphere (n=193) and the North Pacific (n=21). Haplotype diversity of the Colombian humpback population was high relative to other sampled populations, with 37 distinctive haplotypes, 11 of which were represented by a single animal. Both RAPD and mtDNA sequence data suggest further genetic substructure within the Colombian Pacific Coast humpback whale population. A large proportion of haplotypes (n=17) are shared with humpback whales sampled off the Antarctic Peninsula, suggesting a strong migratory connection between these regions as reported elsewhere. Only three haplotypes were shared with other Southern Hemisphere breeding grounds. Two Colombian haplotypes were common to populations from the North Pacific, supporting the hypothesis of a past or present East Pacific gene flow corridor between Northern and Southern Hemisphere populations. □ *Megaptera novaeangliae*, population structure, RAPD, mitochondrial DNA.

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The Colombian winter breeding ground, located between 2-3° north of the Equator off the Pacific Coast, has particular importance as a possible corridor of migratory overlap and genetic exchange between Northern and Southern Hemisphere humpback whale (*Megaptera novaeangliae*) populations of the eastern Pacific (Townsend, 1935; Flórez-González et al., 1998). Olavarria et al. (2000) suggested a migratory

connection between overwinter sites off the Colombian Pacific coast and feeding grounds off the Antarctic Peninsula, based on photo-ID comparisons (Stone et al., 1990) and supported by mitochondrial data (Baker et al., 1998a). This research is one aspect of a long-term investigation of the Colombian Pacific Coast humpback whales by the Colombian non-governmental organisation Fundación Yubarta. In part, 144 skin

samples were obtained between 1991-1999 in two sampling locations (subregions), Gorgona Island and Málaga Bay (Fig. 1).

Whales are observed in this area from mid-June, peaking between August and October, until early December. This study reports the first genetic characterisation of this population using two molecular techniques, RAPD (Random Amplified Polymorphic DNA) patterns and comparative nucleic acid sequence analysis of a fragment of the mitochondrial control region (D-loop).

### METHODS AND MATERIALS

**DNA EXTRACTION.** DNA was extracted from 144 skin samples obtained by biopsy darting or sloughed skin from 1991-1999. For biopsy darting, a small dart was fitted to an arrow (Lambersten, 1987). Sloughed skin was collected using a small nylon net (Amos et al., 1992). Three extraction protocols were used at different stages of the study: Sambrook et al. (1989); the 'QIAmp Tissue Mini Kit' protocol (Qiagen, Inc.); or the 'RapidPrep Micro Genomic DNA Isolation' (Amersham Pharmacia).

**RAPD PROCEDURE.** Four out of six short random primers (10 bp) were chosen for variable, reproducible banding patterns, after an initial screening. These primers were applied to an initial set of 32 Colombian humpback whale samples, as part of a preliminary study (Caballero, 1999). The primers were: P-1 (5'-GGTGC GGGA-3'), P-3 (5'-GTAGA CCGT-3'), P-4 (5'-AAGAG CCGT-3'), P-6 (5'-CCCGT CAGCA-3') (Amersham Pharmacia Biotech). The PCR reaction mix 'Ready-to-go RAPD Analysis Kit' was used under the following low stringency amplification conditions: an initial denaturation cycle at 94°C for 2 minutes, 94°C for 1 minute, 62°C for 1 minute, 72°C for 2 minutes, 45 times. A final extension cycle was performed at 72°C for 5 minutes. PCR products were visualised in polyacrilamide gels stained with a silver solution. Dried gels were scanned and the migration rate (Rf) of each band was obtained. Comparing molecular weights of different bands (50 total) for each individual, a 0-1 matrix (presence-absence) was built. An outgroup set included two species of dolphins (*Tursiops truncatus* and *Stenella coeruleoalba*), two artiodactyl species, hippopotamus (*Hippopotamus amphibius*) and bull (*Bos taurus*) and a sample of human (*Homo sapiens*). Using this matrix, we calculated Jaccard's Genetic Distance

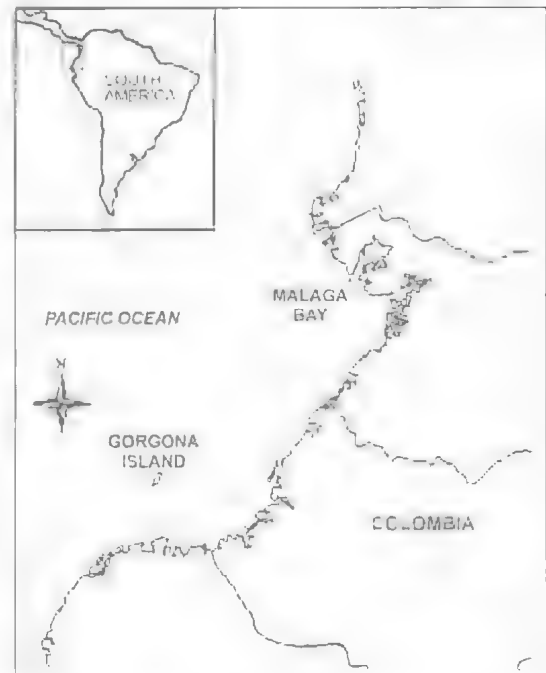


FIG. 1. Colombian winter breeding grounds, showing the two sampling subregions, Gorgona Island and Málaga Bay.

Coefficients by the UPGMA algorithm (Li, 1997) with SYNTAX 5 software. Jaccard's Genetic Distance was calculated as  $D_{ij} = 1 - [C / (2N - C)]$ , where C is the number of common bands between individuals i and j, and N is the number of bands that are different in the two individuals. A consensus parsimony tree was built using the heuristic search option in PAUP version 4.02 software (Swofford, 1993).

**D-loop SEQUENCES.** For all 144 samples (the same 32 samples, and 48 additional samples), an ~550 base-pair fragment of the beginning of the mtDNA control region was amplified by PCR using standard reaction conditions (Saiki et al., 1988). Humpback whale samples from 1992 and 1996-99 field seasons were amplified with primers provided by R. LeDuc of the Southwest Fisheries Science Centre, La Jolla, California: TRO, a light strand primer, which spans portions of the tRNAs, threonine and proline, preceding the control region (5'-CCTCCCTAAAGAC TCAAGG-3'); and a heavy strand primer DH6, (5'-AAATACAYACAGGYCCAGCTA-3'). Samples from 1991 and 1995 field seasons were amplified using a different oligonucleotide primer pair that generated an overlapping

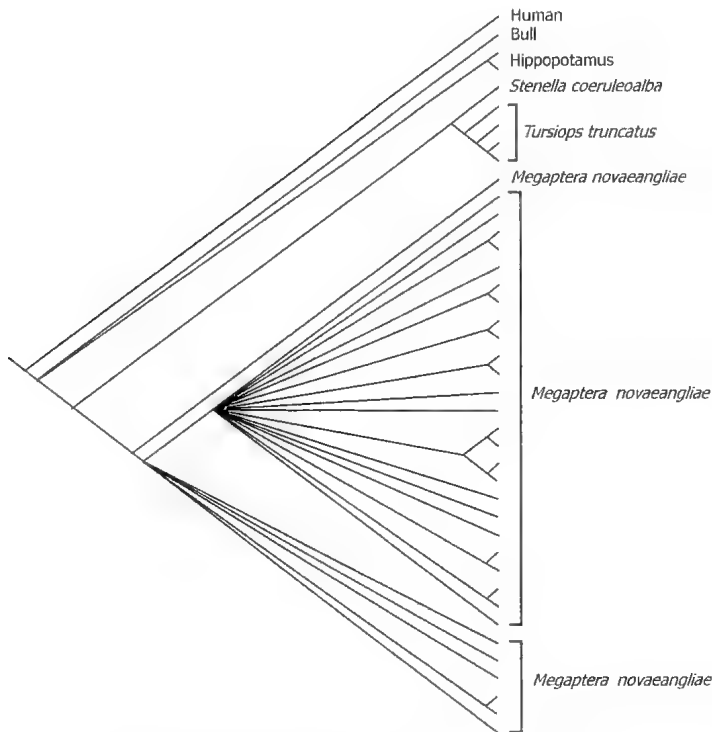


FIG. 2. Strict consensus tree from 194 trees of 263 steps.

fragment of the control region: light strand t-Pro-whale (5'-TCACCCAAAGCTGR ARTTCTA-3'), and heavy strand Dlp5 (5'CCATCGWGATGTCTTATTTAAGRGGAA-3'). Cleaned PCR products were sequenced on an ABI 377 automated sequencer using standard protocols of Big Dye™ terminator sequencing chemistry. Samples were sequenced in both directions to ensure homology of the obtained sequence. Sequences were reviewed and aligned using Sequencher 3.0 software (Genes Code Corporation). For comparative analysis with previously studied humpback whale populations from Colombia ( $n=64$ ), other Southern Hemisphere regions ( $n=193$ ) and North Pacific ( $n=21$ ), sequences were truncated to correspond with a 283 bp segment (Baker et al., 1993; Baker et al., 1998b). Identification of differences among sequences and determination of haplotypes was performed using McClade ver. 3.04.

## RESULTS

Fifty molecular markers or bands, chosen for their reproducibility, obtained from the RAPD method were included in the analysis. Jaccard's Genetic Distance value, determined among individuals of the species *Megaptera novaeangliae*,

was approximately 0.56. This value, compared with those obtained between two delphinid species (0.58), can be interpreted as high for individuals of the same species (Caballero, 1999). As shown in the consensus tree (Fig. 2), the RAPD analysis of 32 individuals of *Megaptera novaeangliae* from Colombia identified three distinctive groups; one classifying possibly closely related individuals, the other two as unresolved groupings of individuals. Three other distinctive branches of the tree classified the delphinid species, clearly separated from the *Megaptera novaeangliae*, the artiodactyl species and the human sample as separate clades.

Mitochondrial control region sequence analysis revealed 37 haplotypes for the Colombian winter breeding ground. Sixteen were unique to this population (Table 1); 9 were shared with the Antarctic Peninsula feeding ground; 3 with other regions in the Southern Hemisphere; 7 with the Antarctic Peninsula and other regions in the Southern Hemisphere; and 2 with regions in the North Pacific, one of them shared also with the Antarctic Peninsula feeding ground (Caballero et al., 2000). The most common haplotype found in the Colombian winter breeding ground was shared with the Antarctic Peninsula but not with any other Southern Hemisphere location.

## DISCUSSION

Randomly Amplified Polymorphic DNA (RAPD) is a molecular technique that has seldom been applied in studies of genetic variation in cetaceans. Analysis of RAPD markers among northern hemisphere minke whales (*Balaenoptera acutorostrata*) revealed the presence of two distinct stocks in the North Pacific and the North Atlantic, and the possible presence of only one breeding stock in the North Atlantic (Martinez & Pastene, 1999). Here we report the first use of RAPD analysis in humpback whales. These results indicate that a reasonable first approximation of population genetic variation may be obtained by application of the relatively fast and inexpensive method of RAPD analysis. These RAPD patterns

TABLE 1. Haplotypes of humpback whales sampled from Colombian winter breeding grounds detected among the 283 bp world-wide mtDNA Control Region consensus region sequences. • = same base as first sequence; – = presumed deletion; ? = unresolved; GI = Gorgona Island; BM = Málaga Bay.

Haplotype	MtDNA Haplotypes and polymorphic sites							No. of Individuals		
	10	20	30	40	50	60	70	Subregion		
	[							GI	BM	Total
GI9101	-CG--GCCT-C-AGCTCCACTTTT	TTTAAATAGTGCCCAATAGGTT	CATTGACTCTCTAGCTGCGACTCTCTC	[68]	13	21		34		
GI9105	-.--C--G.T.T.	.....A..T.	.....C.G.C.A.	.....AC.....C...	[68]	2	1	3		
GI9110	-.--C--T.T.	.....T.....T...	A..C.....C.C...	[68]	3	4	7			
GI9116	-.--T.....C..CC..C.....C...	[68]	2		2					
GI9117	-.--T.....A..T.....C.....C...	[68]	4		4					
GI9112	-.--G.T.T.T.....T.....T...	A..C.....C...	[68]	2	1	3				
GI9124	-.--T.....T.....T.....C...	[68]	2	6	8					
GI9125	-.--T.T.....CT.....C.....C...	[68]	2	2	4					
GI9136	-.--T.....A.C.....C.....CT..	[68]	3	4	7					
GI9130	-.--A..T.....T.....C...	[68]	5	7	12					
GI9142	-.--T.....C.....C.....C...	[68]	1		1					
GI9105	-.--T.....T.....A..C.....CGC.....	[68]	2		2					
GI9105	-.--T.T.....T.....T.....A..C.....	[68]	2	8	10					
GI9118	-.--A..T.....CT.....C.....C...	[68]	1		1					
BM9617	-.--A..T.....CT.....C..G.....C...	[68]	2	7	9					
BM9631	-.--T..C.....T.....T.....A..C.....C...	[69]		3	3					
BM9634	-.--T..C.....C.....C.....C.....C...	[68]		2	2					
BM9614	-.--G.T.T.T.....T.....T.....A..C.....C...	[68]		4	4					
BM9610	-.--A..T.....T.....A.....C.....C...	[68]		1	1					
BM9619	-.--C..T.T.....T.....CT.....C.....C...	[69]		2	2					
BM9611	-.--T..C.....T.....T.....A.....C.....C...	[69]		3	3					
BM9831	-.--T.....T.....C.....C.....CT..	[68]		2	2					
BM9604	-.--T.....C.....T.T.....A.....C.....C...	[68]		2	2					
BM9537	-.--T.....T.....T.....C..A..C.....C.....CT..	[68]		3	3					
BM9502	-.--T.....T.....T.....C.....C.....C...	[68]		2	2					
BM9536	-.--T.T.....T.....CT.....C.....C.....	[68]		2	2					
GI9106	-?-T..C.....T.....T.....T.....A.....C.....C...	[69]	1		1					
GI9107	-?-T..C.....T.....C.....T.....C..A..C.....C.....	[68]	1		1					
GI9111	-?-C--G.T.T.....A..T.....C..C.A.....AC.....C...	[68]	1		1					
GI9132	-?-T.....T.T.....T.....C.....A.....C.....C...	[68]	1		1					
GI9137	-.--T.....A..C.....C.....C.....C.....	[68]	1		1					
GI9211	-.--T.T.....T.T.....T.....A.....G.....C.....	[68]	1		1					
GI9217	-.--T.....C.....C.....C.....C.....C...	[68]	1		1					
GI9222	-.--T.T.T.....T.....T.....T.....A.....C.....C...	[68]	1		1					
BM9637	-.--T.T.T.....T.T.....T.....A.....C.....C...	[68]		1	1					
BM9823	-.--T..G--T.....T.....C..A..C.....C.....G..G.C.T.G.	[68]		1	1					
BM9833	-.--T.....C.....C.....C.....C.....C...	[69]		1	1					
Total Number of sampled individuals								144	144	144

suggest three groupings among Colombian humpback whales. These groupings could indicate further genetic sub-structuring on the Colombian wintering grounds, perhaps as a result of 'hidden stock' structure (Baker et al., 1998b).

Half of the mtDNA haplotypes identified in Colombia are shared with animals that spend austral summers feeding off the Antarctic Peninsula. The migratory connection between these two locations is thus highly supported, as established by Caballero et al. (2000) and Olavarria et al. (2000). The large number of

shared haplotypes suggests this connection extends to the historical past and supports the migratory site fidelity hypothesis proposed by Baker et al., (1990).

The Pacific Coast of Colombia may be the point of transition for trans-hemisphere migration events as suggested by the presence of two haplotypes found in Colombia that are shared with animals sampled in the Pacific as far north as California and Japan. As the only documented overwintering site for Southern Hemisphere humpback whales located north of



the Equator, Colombian waters are uniquely situated to promote migration or genetic exchange between the northern and south-eastern Pacific. These shared haplotypes provide evidence to support the 'genetic corridor' hypothesis, which suggests past and/or present migratory connections between the eastern South Pacific and North Pacific humpback whale populations.

Combining the results of the two molecular techniques, we conclude that humpback whales that overwinter off Colombia's Pacific Coast represent a unique and diverse breeding population. Genetic characterisation of this population describes a group of animals represented by diverse maternal lineages, with high present day fidelity to this breeding site, but clear evidence of historical gene flow from other South and North Pacific Ocean stocks.

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## TRANS-OCEANIC POPULATION GENETIC STRUCTURE OF HUMPBAC WHALES IN THE NORTH AND SOUTH PACIFIC

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We examined genetic diversity of humpback whales in the North and adjacent South Pacific Oceans to investigate the history and dynamics that resulted in their current population structure and for which trans-oceanic gene flow is a phenomenon of great importance. Analysis of mitochondrial DNA variation suggests that humpback whale populations are subjected to contraction and expansion cycles associated with glaciations. Contrast between nuclear and mitochondrial genetic diversities show that expansion phases may be related to regional differentiation dependent upon sex-biased dispersal. To explain trans-oceanic gene flow from sex-biased dispersal, we analysed the species' wintering habits in the Mexican Pacific as described from the sex composition and temporal profile of social groupings. In consideration of the energetic burden for reproduction of female humpback whales and the resultant pre-copulatory competition among males, trans-oceanic gene flow may be explained by changes in winter distribution driven by male dispersal dynamics and gametic exchange across high productivity areas close to the equatorial coast of the American Pacific, as well as by the influence of long-term climatic change in forming trans-equatorial corridors for female interchange. Because of the sensitivity of humpback whale reproduction and dispersal to environment perturbations, our results raise concerns about the effects of climate change on the phylogeographic structure and thereby the evolution and long term conservation of this species. □ *Humpback whale, gene flow, climate change, genetics.*

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In winter, humpback whales, *Megaptera novaeangliae*, return from high latitude summer feeding grounds to warm ca.25°C shallow waters in low latitudes (Dawbin, 1966). Although not well understood, the basis for this preference seems related to breeding, giving birth in an environment suitable to the thermoregulatory capabilities of newborns and for protection of calves from predators (Brodie, 1977; Lockyer & Brown, 1981). Because of the apparent dependence

on water temperature in winter, the breeding ecology of humpback whales may be affected by climatic change. The Pacific coast of the Americas offers a unique biogeography for the study of this process and its influence on population history and structure.

The American Pacific coast bounds, from subpolar latitudes to the equator, the cool and highly productive streams of California and Humboldt which enhance primary productivity

around the equator by upwelling. In relation to coastline topography, the Humboldt Current extends north of the equator while the California Current swings westwards at Baja California Peninsula (Wyrki, 1967; Love, 1975). As a result, humpback whale wintering grounds from Northern and Southern Hemispheres overlap in Central America (Acevedo & Smultea, 1995; Flórez-González et al., 1998; Calambokidis et al., 2000). Pacific Ocean born El Niño and La Niña oscillations provide a source of environmental variation that allows examination of changes in the ecology of migration that have driven the population history of North and South Pacific humpback whales as inferred from genetic analyses.

Elsewhere (Medrano-González et al., 1995; Baker & Medrano-González, in press), we have hypothesised that humpback whale populations are subjected to contraction/expansion cycles associated with glaciations. Apparently, on the American Pacific coast, during glacial times humpback whale populations may have been reduced by restricted feeding areas, a result of an extended ice front forcing distribution closer to the equator. Together with a reduced area of warm waters around the equator, this may have facilitated exchanges between Southern and Northern Hemisphere populations. During deglaciations, the feeding areas of humpback whales increased as the ice fronts retreated and the growing populations dispersed into new breeding areas for which the combination of philopatry and dispersal generated the hierarchical phylogeographic structure observed today. This phenomenon may account for the recent origins of the Hawaiian stock at the end of the Little Ice Age as the coastlines of southeast and central Alaska opened for humpback whale feeding during the 18th and 19th Centuries (Herman, 1979). The Atlantic Ocean had a particular distribution of oceanographic conditions during glaciations with the North Atlantic being very cold with warmer temperatures of ~25°C in the Caribbean Sea (Ruddiman, 1987; COHMAP members, 1988; Williams et al., 1993). Thereby, the pattern of mitochondrial (mt) DNA diversity suggests that the current North Atlantic population of humpback whales has been largely introgressed by the Southern Ocean population through the Caribbean Sea. A study of nuclear genetic variation may provide further evidence to evaluate the extent and timing of the proposed recolonisation of humpback whales in the North Atlantic Ocean (Congdon et al., 2000; Baker & Medrano-González, in press).

The population history and structure of humpback whales is not solely a story in itself but also an enquiry into the interaction between the physical and biological factors that shape the phylogeographic structure and evolution of the species. Here we study the trans-oceanic population genetic structure of humpback whales looking for a set of interactions between different phenomenological levels that may be useful to understand the process of genetic differentiation in general. Such a search is possible by examining the history and mechanisms of trans-oceanic gene flow between the winter of one hemisphere and the winter of the other. Thus, to understand trans-oceanic migration, we should rely on the wintering habits, especially in terms of dispersal and changes in distribution. Here we concentrate on the Pacific coast of the Americas which has two humpback whale populations exhibiting gene flow between them and hierarchical differentiation within each (Medrano-González et al., 1995; Baker et al., 1998a,b; Baker & Medrano-González, in press). We review past publications, recent thesis works developed in México and unpublished data to describe the history and dynamics of gene flow along this coast. Comprehension of this phenomenon may provide insight into the future consequences of global climate change on the evolution of humpback and other baleen whales. Since we made a first approach to understand population history and phylogeographic structure from the habits and ecology of individuals, we invoked the dynamical systems theory which is briefly reviewed in the Appendix.

## METHODS

**GENETIC ANALYSIS.** Skin samples of humpback whales were collected in waters of the Bransfield and De Gerlache Straits in Antarctica, the Colombian Pacific, the Mexican Pacific mainland coast, Socorro Island from the Revillagigedo Archipelago, the Southern coast of Baja California, the Californian coast, the Hawaiian Archipelago and the southeast Alaskan coast. Mitochondrial genetic diversity has been analysed by sequencing and determination of restriction fragment length polymorphisms (RFLP) of a ~400BP segment from the mtDNA control region adjacent to the tPro gene. Nuclear variation was described by genotypes of four microsatellite loci: TAA 31, GATA 28, GATA 53 and GATA 417 (Palsbøll et al., 1997a). Data and techniques have been described by Baker et al. (1993, 1994, 1998a,b), Medrano-González (1993),

Medrano-González et al. (1995), Olavarria-Barrera (1999) and Baker & Medrano-González (in press). Original data still to be described are from Baker (unpubl. nuclear genetic data from Colombia, California, Hawaii and southeast Alaska), Robles-Saavedra (unpubl. mtDNA and sex identification data from México) and Vázquez-Cuevas (unpubl. nuclear genetic data from México). We used these data in a preliminary examination of sex-biased dispersal at different levels of population structure in the American Pacific (Fig. 1). Genetic diversity was described by Nei's index  $h$  (1987: 177) and population differentiation was determined from Wright's  $F_{st}$  (1969) as calculated by the variance analysis of Excoffier et al. (1992). Gene flow ( $Nm$ ), the number of interpopulation migrants per generation, was estimated by the following Wright's (1969) approximation:

$$Nm = \frac{1}{P} \left( \frac{1}{F_{st}} - 1 \right) \quad (1)$$

where the ploidy factor  $P$  equals 2 for mtDNA and 4 for nuclear genetic markers.

To calculate population expansions and clade divergence dates, the distribution of mtDNA coancestry time was analysed from the sequence data compiled by Baker & Medrano-González (in press) considering a nucleotide substitution rate of 1% per million years (MY), a male/female ratio of 1:1 and a female generation time of  $t_g=10$  years (Chittleborough, 1958, 1965; Clapham & Mayo, 1987a,b; Hoelzel et al., 1991; Baker et al., 1993; Clapham et al., 1993; Martin & Palumbi, 1993; Clapham, 1996) (Fig. 2). This approach assumes that the molecular clock is valid at population divergence time scales and thereby that population history dates depend mostly on population fragmentation/bottlenecking events. MtDNA coancestry-time distributions ( $p_i$ ) were fitted to the following equation (Avise et al., 1988; Rogers & Harpending, 1992):

$$p_i = \left( 1 - \frac{1}{N_f} \right)^i \quad (2)$$

where  $N_f$  is the long term effective population size as number of females and  $t$  is time in generations. We also tested whether the analysed fragment of mtDNA was neutral using Tajima's D test (1989a,b). A simulation for the expansion of the private mitochondrial haplotype most abundant in the Mexican mainland Pacific coast (AE) was performed to estimate the divergence

time between this aggregation and that of the Revillagigedo Islands (Fig. 3). We also estimated the coancestry time of mtDNA lineages to describe the divergence among two haploid populations due to genetic drift, starting from  $F_{st}=0$ , with the following equation, adapted from Weir (1990: 167), at time  $t$ :

$$F_{st(t)} = 1 - \left( 1 - \frac{1}{N_f} \right)^t \quad (3)$$

The software 'Arlequin' 1.1 (Schneider et al., 1997) was used for most genetic calculations. Curve fitting was made with the least-squares procedure available in 'Sigmaplot' 1.02. Simulations were performed using the software 'Deriva', developed by Medrano-González (1993) and available upon request.

**WINTERING HABITS ANALYSIS.** Bahía Banderas in the Mexican mainland Pacific coast and Socorro Island from the Revillagigedo Archipelago were visited for humpback whale research from January to April, 1999. Observations on Socorro Island in this year were carried out with the logistic support of Salvatore Cerchio from the University of Michigan. Wintering habits of humpback whales were described by the occurrence profiles of pod and activity classes. A consensus definition of such classes follows based on Tyack & Whitehead (1983), Baker & Herman (1984), Baker (1985), Mobley & Herman (1985), Glockner-Ferrari & Ferrari (1990), Clapham et al. (1992), Medrano et al. (1994), Brown & Corkeron (1995) and Darling & Bérubé (2001). These are: 1) Solos – juvenile and adult animals of both sexes which mostly transit between conspecific groups; 2) Singers – adult males which stay in a definite area for many hours vocalising songs to attract receptive females and/or to order social status; 3) Adult and/or juvenile pairs – allied males or a male and a female associated around mating; animals generally in transit (pairs of females seem to be very infrequent and unstable pods); 4) Female with a newborn; 5) Female with a newborn and escort – the escort being an adult or juvenile male presumably awaiting the oestrus of the cow; 6) Groups – three or more adults or juveniles; a calf and cow may be present. Humpback whale groups have been described as groups of males in competition. There is normally a nuclear female around which males exhibit agonistic behaviour. Agonistic interactions in groups, however, may occur without a female present.

Sex composition of pods was determined using the method of Palsbøll et al. (1992; Medrano et al., 1994; Robles-Saavedra, unpubl. data). Relative size was judged by eye to distinguish the following classes of sex/reproductive status (*sr*): 1) Newborns; 2) Juvenile or adult males; 3) Juvenile or adult non nursing females; and 4) Nursing females. Temporal profiles of humpback whales wintering in the Mexican Pacific were analysed weekly and relative abundance was determined from the number of sightings per hour of boat-based search and observation (Fig. 5). Abundance of each sex/reproductive status class ( $f_{sr}$ ) was calculated combining the data of sex composition and occurrence of pods as follows:

$$f_{sr} = \sum_g f_g N_g Q_{srg} \quad (4)$$

where  $f_g$  is the abundance of pod  $g$ ,  $N_g$  is the average size of  $g$  and  $Q_{srg}$  is the fraction of individuals of the class  $sr$  in  $g$  (Table 1). Encounter rate between males ( $m$ ) and females ( $f$ , both nursing and non-nursing) was determined as the product of their respective abundances, i.e.  $f_m f_f$ . Encounter rate between males was calculated as  $f_m^2$ .

## RESULTS AND DISCUSSION

**GLOBAL LINEAGE DISTRIBUTION AND TRANS-OCEANIC GENE FLOW.** Previous descriptions of the global structure of mtDNA variation in humpback whales demonstrate differentiation among and within the three oceanic populations: North Pacific, North Atlantic and Southern Ocean (Baker et al., 1993, 1994; Baker & Medrano-González, in press). Baker et al. (1993) described the grouping of world-wide mtDNA lineages into three clades, referred to as CD, IJ and AE, with categorical and frequency differences in the three oceans. The CD clade was found in each of the three oceans and was numerically dominant in the Southern Hemisphere. The IJ clade was most abundant in the North Atlantic, showing a clinal increase in frequency across feeding grounds from the Gulf of Maine to Norway (Palsbøll et al., 1995; Larsen et al., 1996; Baker & Medrano-González, in press). The IJ clade was present in all regional populations examined to date in the Southern Hemisphere but entirely absent in the North Pacific. The AE clade was most abundant in the North Pacific showing a clinal increase, especially in the subtype A, from a very low

frequency on the California feeding grounds to fixation on the Alaskan feeding grounds. The AE clade was also found in low frequency on the Colombian wintering ground and the Antarctic feeding ground but is absent from other Southern Hemisphere regions and the North Atlantic Ocean (Baker et al., 1993, 1994, 1998a,b; Medrano-González et al., 1995; Baker & Medrano-González, in press).

Although this global distribution of humpback whale mtDNA lineages supports, in general, the assumption of isolation of oceanic populations by continental landmasses and the seasonal opposition of the hemispheres, it also suggests a corridor of gene flow or interchange along the Pacific coast of the Americas. The CD clade is found in high frequency on both Colombian and Mexican wintering grounds, indicating at least past migration from the Southern Ocean to the North Pacific. A smaller frequency of individuals with identical mtDNA haplotypes in both regions suggests more recent gene flow in this direction. Similarly, the low frequency of the AE clade in Colombian and Antarctic Peninsula region suggest a lower rate of historical exchange from the North Pacific to the south (Fig. 1).

For microsatellites, very similar patterns of molecular size distribution are observed in the Antarctic Peninsula and along the American Pacific coast. In general, nuclear genetic markers exhibit a smaller differentiation, as compared with mtDNA, within and between oceanic populations (Palumbi & Baker, 1994; Valsecchi et al., 1997; Baker et al., 1998b) suggesting that male gene flow is larger than that of females (Fig. 1). These patterns support the idea that nuclear genetic markers provide a historical perspective different from that of mtDNA (Congdon et al., 2000). Because variation of microsatellites consists basically on the number of oligonucleotide repeats, these genetic markers evolve with a high degree of homoplasy and their analysis is thus poorly informative for phylogenetic inferences. However, microsatellite mutations yielding imperfect repeats generate different repeat frames which may identify different allelic lineages and thus, dispersal events as well as mutation trends. In humpback whales from the American Pacific, for example, four repeat frames may be found in the locus GATA28. Described with the molecular size of the PCR products based on the primers of Palsbøll et al. (1997a), these frames are 147-155BP, 156-176BP, 154-190BP and 185-189BP. Given the geographic and molecular size distributions of each frame and assuming that

TABLE 1. Composition of sex and reproductive status classes ( $Q_{\text{sex}}$ ) for different humpback whale pods in the Mexican Pacific. Males and non nursing females include juveniles and adults. Data from Medrano et al. (1994) and unpublished results of Robles-Saavedra. \* 6 adults sampled, all females; \*\* 5 assumed escorts, males, and 9 assumed cows, females; \*\*\* N = number of animals in the pod.

Pod	Sample size	Newborns	Males	Non nursing females	Nursing females
Solo	11	-	0.73	0.27	-
Singer	3	-	1.00	-	-
Pair	32	-	0.78	0.22	-
Cow/calf*	6	0.50	-	-	0.50
Cow/calf/escort**	14	0.33	0.33	-	0.33
Group	55	-	0.87	0.13	-
Group/calf***	-	1/N	(N-2)/N	-	1/N

such frames are originated by 3BP imperfect repeats of the GATA 28 tetramer, we have built an hypothetical evolutionary pathway between the four repeat frames (Fig. 1). This pathway shows that the repeat frame lineage 185-189BP has originated from the alleles 182BP or 186BP recently in the east South Pacific and has not migrated to the east North Pacific. Thus, coalescent models using the frequency of the private alleles (see below) could give an estimate for the most recent separation between the North and South Pacific. For the locus GATA 53 the frames 195-199BP, 201-209BP and 202-210BP have been found in the Mexican Pacific only, providing an opportunity to estimate the divergence between these wintering aggregations and those of Hawaii (Fig. 1). The evolutionary pathways illustrated show that some microsatellite lineages have recently originated, as the frame 185-189BP of locus GATA 28, while others may be reminiscent, as the frame 156-176BP of locus GATA 28 which is rare, as well as widely but discontinuously distributed in both molecular size and geography. Since the apparently most recent frame lineages (those with short and continuous molecular size and geographic distributions) are longer than the apparently older frame lineages (Fig. 1), a general trend of increase in microsatellite size may be deduced from our analyses according to what is apparent also in other mammals (Rubinsztein et al., 1995). Cloning and sequencing of the different microsatellite alleles is necessary for a proper phylogenetic interpretation of the repeat frames and thus a comprehensive analysis of these topics need to be developed elsewhere.

**RECENT AND HISTORICAL POPULATION CHANGES AND TRANS-OCEANIC GENE FLOW.** For North and South Pacific humpback whales, and for separate CD and AE types,

Tajima's (1989a,b) neutrality test shows a deficiency of nucleotide differences between individuals as expected from the number of polymorphic sites in the examined fragment of mtDNA. This suggests that mtDNA variation of humpback whales in the North and South Pacific has been affected by a population reduction. In order to know whether this reduction of genetic diversity is related to exploitation by humans we may consider an exploitation worst-scenario for the species in the North Pacific with  $N_f = 250$  following Rice (1974) and considering a male/female proportion of 1:1 during 10 generations (100 years). Following Wright's formulation (1931: 111; Nei, 1987: 360), genetic drift in these conditions is expected to have diminished mtDNA diversity to a proportion of  $H_t/H_o = (1 - (1/N_f))^t = 0.96$  from its original value ( $H_o$ ). Consideration of the levels and geographic patterns of mtDNA variation world-wide also indicates that humpback whale genetic diversity has not been much affected by humans (Baker et al., 1993, 1994). Therefore, humpback whale mtDNA variation keeps information about historical fluctuations of gene flow, population fragmentation and abundance.

The mtDNA coancestry distribution of humpback whales world-wide shows two expansion waves, with mean times of ~230,000 and ~1,500,000 years, assuming a substitution rate of 1% per million years (MY), which correspond to intra and interclade variations respectively (Fig. 2). To analyse single expansions, we have then examined intraclade and intrapopulation variation fitting the mismatch distribution to equation (2) according to Avise et al. (1988). Average coancestry times in the North Pacific are 145,000 years for the AE clade and 130,000 years for the CD clade. Insufficient data exist to analyse the mismatch distribution of AE types in the



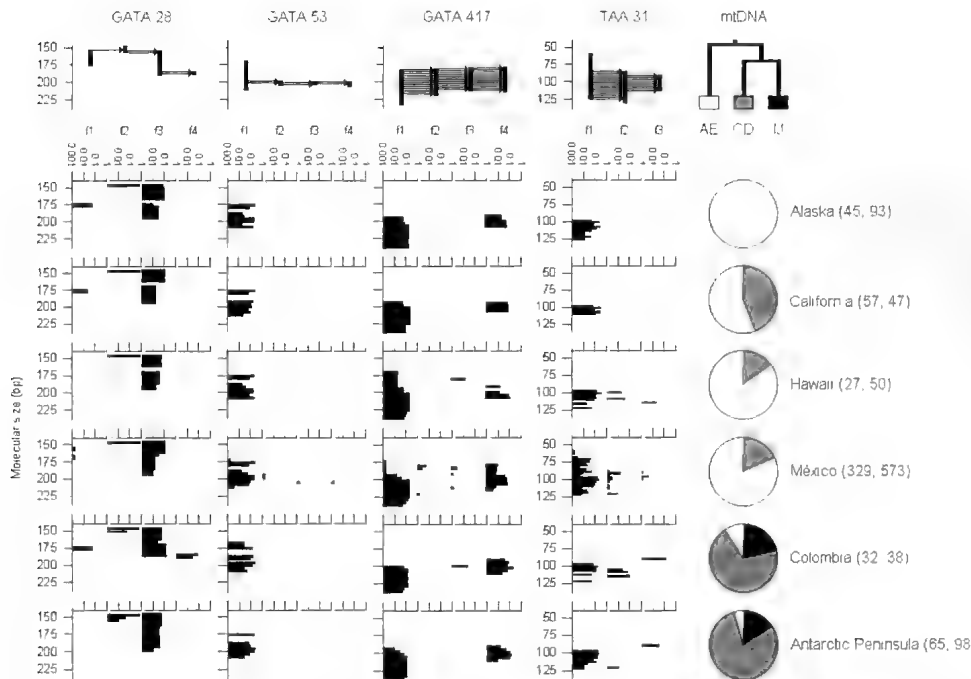


FIG. 1. Genetic variation of mtDNA control region and 4 microsatellite loci in humpback whales from the American Pacific coast and the Antarctic Peninsula. Parentheses indicate sample size as number of mitochondrial haplotypes and average number of microsatellite alleles per locus. Distribution of microsatellite molecular size in base pairs (bp) is plotted for the 3 or 4 sequence repeat frames (f1, f2, f3 and f4). Frequency scale for each frame is logarithmic from 0.001-1. Phylogeny of the three main mtDNA clades and evolutionary pathways between the different microsatellite repeat frames are sketched in the top indicating with arrows all possible mutations of 3BP imperfect repeats for the GATA tetramers and mutations of 2BP imperfect repeats for the TAA trimers. Polarity from f1 to f4 or f3 has been hypothesised on the basis of molecular size and geographic distribution. Repeat frame lineage intervals are, respectively for f1, f2, f3 and f4, 156-176BP, 147-155BP, 154-190BP and 185-189BP for GATA 28; 168-212BP, 195-199BP, 202-210BP and 201-209BP for GATA 53; 182-234BP, 181-221BP, 180-212BP and 179-215BP for GATA 417; 59-125BP, 88-130BP and 90-114BP for TAA 31. MtDNA data are from Baker & Medrano-González (in press), Olavarria-Barrera (1999) and unpubl. results of Robles-Saavedra. Nuclear genetic data are from Olavarria-Barrera (1999) and unpubl. results from Baker & Vázquez-Cuevas.

Southern Ocean but they have a coancestry mean time of 110,000 years. The CD clade in the Southern Ocean has a bumpy-bell shaped distribution with mean of 950,000. These distributions roughly correspond to long term effective population sizes of over 14,000 females in the North Pacific and over 90,000 females in the Southern Ocean which exceed the pristine population size estimates of Rice (1974) and Chapman (1974) (Fig. 2). Coalescence within the North Pacific of AE and CD clades dating back 110,000-145,000 years corresponds to the end of Illinoian glaciation (Lorius et al., 1985). Phylogenetic analysis of mtDNA variation indicates that multiple and reverse trans-oceanic gene flow events have occurred at least for CD types. This

suggests a minimum of two trans-oceanic intermingling periods related to the Illinoian and Wisconsinian glaciations (Baker & Medrano-González, in press).

**WITHIN OCEAN DIFFERENTIATION: ORIGINS OF THE OFFSHORE REVILLAGIGEDO BREEDING GROUNDS.** Humpback whales from Revillagigedo Islands and from the Mexican Pacific coast are separate subpopulations which, being genetically similar, have presumably diverged recently from each other (Medrano-González et al., 1995; Urbán et al., 2000). Nucleotide mtDNA divergence between Mexican coast and Revillagigedo grounds is 0.018% which suggests a divergence time of 9,000 years considering a substitution

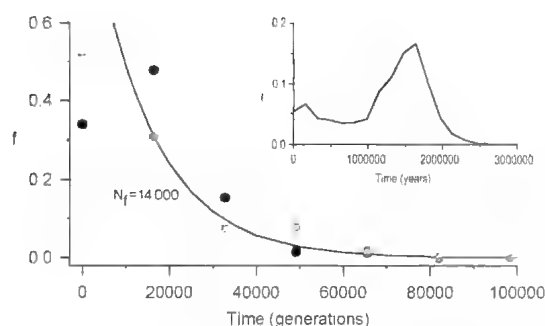


FIG. 2. Distribution of coancestry times for the mitochondrial AE (black,  $n = 87$ ) and CD (gray,  $n = 24$ ) clades in the North Pacific. The curve shows the function of equation (2) which fitted  $N_f \sim 14000$  for both distributions. The inside graph shows the world-wide coancestry distribution ( $n = 268$ ). Data from Baker & Medrano-González (in press).

rate of 1%/MY. This reasoning is constrained by the fact that genetic divergence is not due to a gene substitution event but to different haplotype frequencies and by the presence of private haplotypes, such as AE, E2, E3, E4 and F1, in the wintering grounds of the Mexican Pacific coast (Medrano-González et al., 1995). We considered that these types may serve for estimating the divergence time of Revillagigedo whales by looking for the time necessary for a newly arising mutant to reach current observed frequencies. We have simulated the propagation of a mitochondrial and neutral mutant in hypothetical populations of humpback whales of size  $N_f = 5,000$  to 15,000 females, generation time  $t_g = 10$  years and reproductive rate  $B_r = 0.1$  calves/individual, year. We used as reference the AE haplotype, a subtype of the AE clade, which has a frequency in coastal areas of  $q = 0.05$  to 0.07 (Medrano-González et al. 1995; Robles-Saavedra, unpubl. data), since it is the most abundant among coastal private types. For different combinations of reference- $q$  value and  $N_f$ , we made  $2N_f$  simulations. In general, 400 to 900 generations take place for a mutant to reach the current frequency of the AE type (Fig. 3). Also, the current mtDNA differentiation between coastal and Revillagigedo humpback whales is  $F_{st} = 0.11$  (Medrano-González et al., 1995) and the time to attain this value by genetic drift, starting from  $F_{st} = 0$ , was calculated with equation (3) and found to be 874 generations for  $N_f = 7,500$  and 1,748 generations for  $N_f = 15,000$ . In summary, the nucleotide divergence of 0.018%, the origins of the AE haplotype in 400 to 900 generations ago and the attainment of current  $F_{st}$

$= 0.11$ , coincide to a divergence time between humpback whales from the Mexican Pacific coastal grounds and Revillagigedo Islands of 4,000-9,000 years ago which is the last deglaciation period (Lorius et al., 1985; COHMAP members, 1988).

**MALE AND FEMALE GENE FLOW.** The low nuclear genetic differentiation indicates that total gene flow among humpback whale populations is underestimated by equation (1) as it is valid only for small values of the per capita migration rate,  $m$  (Wright, 1969). Because of the much higher differentiation in mtDNA, it may be deduced that a large proportion of the humpback whale gene flow is owed to males (Palumbi & Baker, 1994; Baker et al., 1998b) (Fig. 4). However, for a direct comparison between total gene flow, determined from the population differentiation of nuclear loci and gene flow of females, determined from the differentiation of mtDNA, these genetic markers should have approximately equal mutation and fixation rates and thus, similar levels of diversity. In our data, the gene diversity index  $h$ , is in average for mtDNA 63% of the diversity found in microsatellites and this implies a relatively lower resolution of mtDNA to detect population structure. On the basis of genetic diversity then, mtDNA gene flow may be overestimated if contrasted with gene flow in nuclear loci. Therefore, the inaccurate estimation of total gene flow using equation (1) and the different molecular evolution rates of mtDNA and microsatellites seem irrelevant for a general view of sex-biased dispersal as the proportion of gene flow by males is apparently high and underestimated. Although, in principle, two sets of genetic variation data with different linkage to sex, nuclear and mitochondrial for example, should be enough to get independent estimates of male and female dispersal, the large proportion of males in nuclear gene flow fits their  $1/f$ -dispersal distribution at different population levels ad hoc to equation (1) since  $\sim 1$  (Fig. 4; Appendix). An option to determine population differentiation and gene flow of males independently, is to analyse genetic variation in a haploid fragment of the Y chromosome. Our preliminary analytic expression for male dispersal in Fig. 4, suggests that male dispersal distributes as 'pink noise' and thus that it is associated to a chaotic dynamic process (Bak & Paczuski, 1995; Halley, 1996; Appendix). Female dispersal has no direct relationship with nuclear genetic differentiation. Because of their greater fidelity to migratory destinations, female dispersal should be more

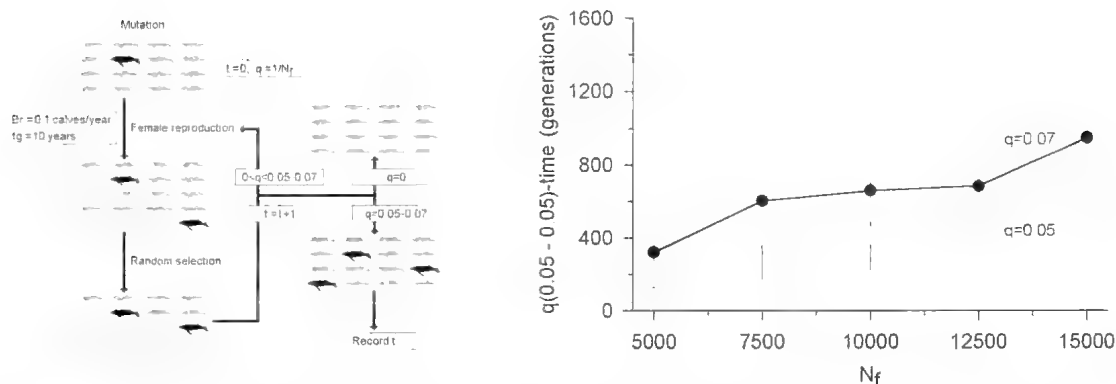


FIG. 3. Simulation of the AE haplotype expansion in the humpback whale aggregation of the Mexican Pacific coast. Left: Individual simulation flow chart starting with the appearance of a mutant (black whale) and showing changing values of time ( $t$ ) and private haplotype frequency ( $q$ ), fixed parameters of population size ( $N_f = 5000$  to 15000), generation time ( $t_g = 10$  years), birth rate ( $B_r = 0.1$  calves/individual, year) and  $q$  reference value (0.05 or 0.07). Two points next to the equality in  $t$  or  $q$  mean that the value in the right side is assigned to the variable in the left. After any generation, the value of  $q$  may be zero (the simulation is then finished and a new one is started), over zero and under the reference value (the simulation goes to a new generation with its reproduction and selection cycle) or reach the reference value (the time as generations elapsed since the mutant apparition is recorded). Right: Simulated time to reach the reference values  $q = 0.05$  or  $0.07$  for variable population size ( $N_f$ ) performing  $2N_f$  simulations in each case. Error bars represent standard deviation of 18 to 58 successful simulations.

subjected to historical contingencies such as a large intermingling between México and Colombia at least during the last two glaciations and an intra-oceanic divergence after the separation of a monophyletic founder group from which the Alaska/Hawaii stock derived at the end of the Little Ice Age (Fig. 4).

Sex biased dispersal of the humpback whale seems to derive from its polygynic mating system. Precopulatory competition among males makes them disperse into breeding areas seeking opportunities to mate while females are more philopatric in relation to energetic burdens for reproduction (Brodie, 1977; Greenwood, 1980; Lockyer & Brown, 1981; Clapham, 1996). The difference in philopatry between sexes is both spatial and temporal. Timing of migration between feeding and breeding areas, in which females stay for a short period in breeding areas or even winter along the migratory route without reaching breeding grounds, optimises the energy assimilation of females for reproduction and the chances of males to mate (Dawbin, 1966; Brown et al., 1995; Craig & Herman, 1997).

**EXPANDING ICE, RETREATING WHALES.** Our results suggest that glaciations have an homogenising effect on humpback whale populations because of habitat reduction and increased trans-oceanic genetic exchange while interglacial periods favour differentiation

through reduced trans-oceanic gene flow and colonisation of regional habitats within oceans. This is contrary to many cases for which glaciations fragment populations in isolated refuges, for example belugas and narwhals (O'Corry-Crowe et al., 1997; Palsboll et al., 1997b). This difference may result from the way glaciations affect the large continuous feeding and breeding habitat of humpback whales, in coasts open to the ocean between the tropics and ice fronts, as contrasted to the more reduced and fragmented habitat of belugas and narwhals in circumpolar coasts and rivers.

Even if glaciations narrow the area of warm waters isolating the east North and South Pacific wintering grounds, the mechanism by which humpback whales from both hemispheres meet or disperse needs consideration. Acevedo & Smultea (1995) have found that humpback whales from the Northern and Southern Hemispheres currently overlap their winter distribution in Central America. Ladrón de Guevara-Porras (2001) observed that humpback whales in the Mexican Pacific have a higher relative abundance where and when sea surface temperature is close to 25°C. The spatial and seasonal distribution of this isotherm is variable as a result of the El Niño/La Niña oscillation. These findings suggest that, driven by climatic change, wintering humpback whales from both hemispheres may

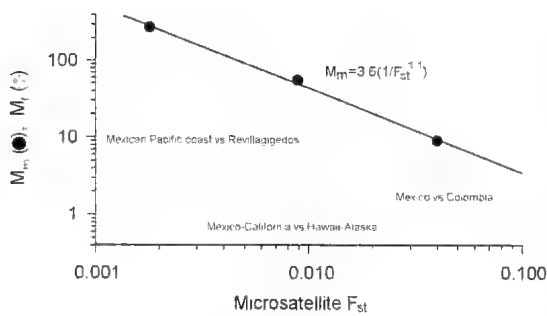


FIG. 4. Sex-biased dispersal of humpback whales at different population structure levels. Female gene flow ( $M_f$ ) was estimated from the  $F_{st}$  for the mitochondrial control region. Male gene flow ( $M_m$ ) was estimated subtracting  $M_f$  from the total gene flow obtained with four microsatellite loci. The function fitted for male dispersal in dependence of population differentiation is shown ( $r^2 > 0.99$ ). MtDNA data are from Baker & Medrano-González (in press) and nuclear genetic data are unpublished results from Baker & Vázquez-Cuevas.

enlarge their temporal and spatial distribution in the wintering grounds of the American Pacific. A critical overlap in the spatial and seasonal distribution of North and South Pacific humpback whales in their wintering grounds around Central America, may thus allow intermingling between these populations. Trans-oceanic nuclear gene flow by males can result from gametic exchange during an early or late winter wandering without dispersing permanently between oceans. Trans-equatorial mtDNA gene flow, however, requires that females themselves, not just their gametes, somehow shift their migratory cycle from the winter of one hemisphere to the other. Considering the seasonal feeding habits of humpback whales, such a migratory shift would require two consecutive winter seasons without a transit to the feeding grounds. Although presumably more difficult than the gametic exchange of nuclear genes, trans-equatorial dispersal and a shift in migratory cycles could be facilitated by the occurrence of highly productive areas close to or in the wintering grounds of the east Pacific such as the Sea of Cortés, the Dome of Costa Rica and other small areas in the coasts of México and Central America (Love, 1975; <http://seawifs.gsfc.noaa.gov/SEAWIFS/IMAGE/S/CZCS.html>). There is increasing evidence that humpback whales feed in winter grounds, especially in colder years when schooling fishes, such as sardines, may be abundant (Gendron & Urbán, 1993). Feeding in wintering grounds is a factor that may increase the spatial and temporal

overlap between North and South Pacific humpback whales favouring trans-oceanic gametic exchange by males. It is known also that a number of humpback whales, not yet demographically identified, spend the summer feeding in the Sea of Cortés (Urbán & Aguayo, 1987). Research on the identity, migration and ecology of mysticetes in the Sea of Cortés (e.g. Tershy et al., 1990), may enlighten such a process.

#### CONTEMPORARY CLIMATE EFFECTS.

Although humpback whales appear to prefer a particular sea surface temperature, at a definite place and time their relative abundance can vary greatly without a defined pattern. Between years and regions, the temporal profiles of pod occurrence and relative abundance are different (Ladrón de Guevara-Porras, 2001) indicating the existence of complex social dynamics. For the 1998/99 winter in the Mexican Pacific, the temporal profiles of the different sex/reproductive status classes (Fig. 5) show a higher abundance of males which changes in parallel with the abundance of non-nursing females, though with a larger variation. Male abundance roughly varied inversely to fluctuations in nursing females except during the late breeding season. This suggests that movements of males in the Mexican Pacific wintering grounds follow the opportunity to find a receptive female and that, being more abundant in breeding grounds, the fluctuation of male abundance amplifies the smaller unpredictable variations of female abundance. Changes in local relative abundance are interpreted as dispersal to neighbouring breeding areas. In general, aggregation of humpback whales changes parallel to the global relative abundance. However, the temporal trajectories of abundance and aggregation follow a complex pattern similar to a strange attractor and which is a wide cycle with Socorro Island (Fig. 6; Appendix). Male abundance in the Mexican Pacific coast is lower and with smaller and more frequent variations compared to Socorro Island (Figs 5, 6). This may reflect the fact that the coastal breeding grounds are a large continuous area between Southern Baja California and the mainland coast which allow whales to move easily and spread all along the breeding ground. The Revillagigedo Islands, however, are small and relatively isolated. Whales here have a higher local relative abundance and move less frequently between islands making dispersal events more rare and abundance/aggregation fluctuations larger and less complex compared to the Mexican Pacific coast (Ladrón de Guevara-Porras, 2001).

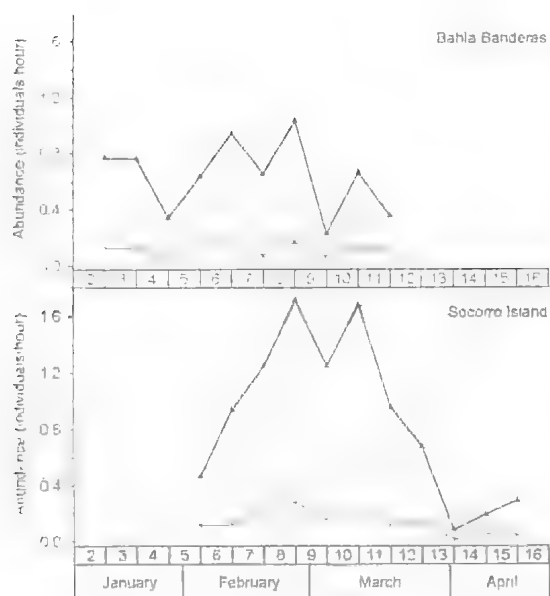


FIG. 5. Relative abundance profiles of males (triangles, black), non nursing females (circles, gray) and calving females (squares, light gray) during the 1999 winter in the Mexican Pacific mainland coast (Bahía Banderas) and the Revillagigedo Archipelago (Socorro Island). Numbered blocks show the weeks elapsed after January 1. The relative abundance of each sex/reproductive status class ( $f_{sr}$ ) was calculated in weekly periods using equation (4). Boat-based observation effort was 234 hours for Bahía Banderas and 269 hours for Socorro Island.

Because of its definition, the encounter rate between males and females increases proportionally with increase in total abundance. Encounters among males, however, vary at a higher rate indicating that local increments of abundance, despite favouring encounters between males and females, greatly increase the intensity of competition among males. The approach of such competition to a critical value may then promote dispersal events and thereby, sudden decreases of local abundance from which abundance/aggregation may rise again (Figs 5, 6). Thus, male competition for mating and dispersal in response to small unpredictable fluctuations in the local abundance of receptive females may drive male gene flow in the border of chaos and therefore generate, in the long term, its  $1/f$ -distribution at different population structure scales (Appendix).

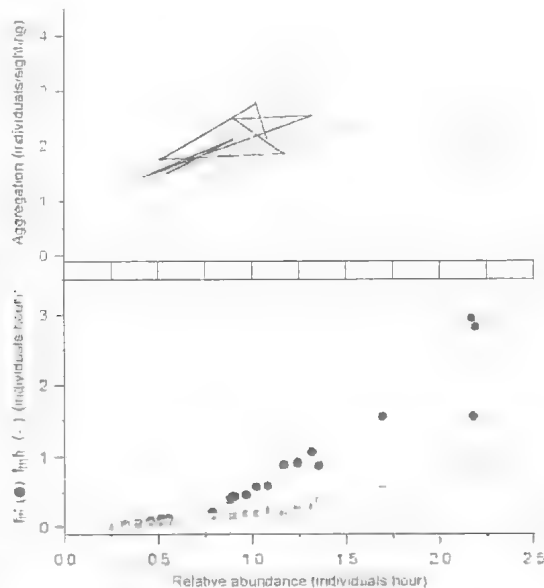


FIG. 6. Interactions among humpback whales, as functions of relative abundance, during the 1999 winter in the Mexican Pacific. Upper graph: Aggregation in Bahía Banderas (black) and Socorro Island (light gray). Lines show trajectories in time. Lower graph: Encounter rates among males ( $f_m^2$ , black) and between males and females ( $f_m f_f$ , light gray).

## DISCUSSION

Global climate change has the potential to affect all marine life through changes on prey availability, areas for breeding and even by the direct physical damage of ultraviolet radiation. Chittleborough (1991) has hypothesised that global warming may severely affect Southern Ocean ecology because of positive feedbacks between disturbances of physical and biological factors among which the  $\text{CO}_2$  sink is critical. For humpback whales, the characteristic winter behavioural displays associated with pre-copulatory competition among males for a low number of receptive females in breeding grounds (Tyack & Whitehead, 1983; Baker & Herman, 1984; Whitehead, 1985; Brownell & Ralls, 1986; Brown et al., 1995; Clapham, 1996; Craig & Herman, 1997), the dependence of warm and coastal waters for reproduction (Dawbin, 1966; Ladrón de Guevara-Porras, 2001) and the association of population history to climate change (Medrano-González et al., 1995; Baker & Medrano-González, in press), may all derive from energetic constraints to female

reproduction. The basis of such restraints is not currently understood though they are known from the study of life history and reproduction and seem related to feeding ecology (Chittleborough, 1958, 1965; Clapham & Mayo, 1987a,b; Straley et al., 1994; Juárez-Salas, 2001). Given the sensitivity of humpback whale reproduction and dispersal to environment variation, climate change in this species may also have an impact through a reduction in periodic trans-oceanic gene flow. Already, severe El Niño events have resulted in large masses of warm water settling along the equatorial Pacific coast of the Americas (Enfield, 1989). Such water masses could obstruct the narrow corridor of gene flow between adjacent regions of both hemispheres, leading eventually to complete genetic isolation and even speciation between oceanic populations. This antitropical mode of population differentiation is actually involved in the speciation of many cetaceans and has been described by Davies (1963) long before genetic data were available. Therefore, in addition to the immediate effects of climate change on the abundance of baleen whale populations, our study on humpback whales raises concern about long-term alterations on the phylogeographic structure and thereby evolutionary potentialities of this and other species inhabiting the eastern tropical Pacific.

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## APPENDIX

### A BRIEF ON CHAOTIC DYNAMICAL SYSTEMS

It is traditionally believed that the complexity of a system's behaviour corresponds to the complexity of its structure and thus to the complexity of a scientific explanation for it. The analysis of complex behaviours is therefore often devoted to statistical dissections of multifactorial relationships and historical accounts of facts which are conceived as accidents as they are considered non repeatable and resulting by chance given a particular conditions set. Studying climate, Lorenz (1963) discovered that some simple systems

may exhibit unpredictable behaviour which, however, is not random and which is now called chaos. Chaos appears in systems having at least a set of opposing processes which, in a critical state, yield a solution very sensitive to small variations. It may be guessed that many phenomena may involve transition to chaos. Indeed, chaos is ubiquitous and it is actually in the very origins of ordered phenomena as life.

Chaotic systems are self similar at different scales; this property is called fractality because the corresponding

geometric sets may have non-integer dimensions. The circulatory system, for example, is a branching set with topological dimension of 3 but is functionally a hybrid between volume and area with fractal dimension of 2.4. The chaotic dynamics underlying biological functions and its dimensional hybridism is the very basis for the pervasion of allometry in biology. Another property of chaotic systems is adaptation. Heart rate, for example, is chaotic and this allows the organism to adapt to a changing and unpredictable environment. Genetists know the importance of genetic diversity for the evolutionary adaptation of species being such a diversity a fractal branching set of cladogenetic processes. In general, organisms as replicative systems away from thermodynamic equilibrium live in the border of chaos and are adaptive.

A dynamic system is any whose behaviour changes in time. The examination of such systems includes the temporal profile of quantities which describe the system's behaviour and also the relationship between its independent variables. The plot of those variables is called phase-space. When the system has only one variable, the state at time  $t$  is related with the state at time  $t+\tau$ . In chaotic systems, trajectories in the phase-space are not predictable. Such trajectories, however, occupy a particular area of the space. The phase-space areas mostly visited by the system are called attractors. If trajectories in an attractor are complex, that is, not closed curves, the attractor is called strange. The distribution of fluctuations size is also of interest. The variation of the quantities used to describe the system is called noise. Thus, the distribution  $1/f^\alpha$  is also called  $1/f^\alpha$  noise where  $\alpha$  is defined by the autocorrelation in the system motions. In a system like a roulette, there is no correlation between consecutive throws and in the long term all possible results will be equally frequent giving a flat distribution in which  $\alpha=0$ . If the roulette results are colors, we may call its distribution as white noise. In a system like a particle in a gas, the position of the particle strongly correlates with its previous position and this correlation is rapidly loss in time. The distribution of motion sizes in a log-log plot is a steeply decaying line with  $\alpha\sim 2$ . The distribution of this Brownian motion is thus called brown noise. In a chaotic system, motions are partially correlated, they

are neither random nor deterministic and the size of fluctuations distributes with  $\alpha\sim 1$ . Pink noise is the term given to these phenomena.

For wintering humpback whales, we hypothesise that competition between males for a low number of receptive females makes them disperse between neighbouring areas (Fig. 5). Dispersion events may probably be in the border of chaos (Fig. 6) making gene flow of males self similar at different scales of population structure. Gene flow of females, instead, seems more subjected to historical contingencies dependent from environment changes (Fig. 4). Modelling of this requires refinement of what the facts are and consideration of a proper spatial structure. It is interesting that the size and continuity of wintering grounds, as contrasted by the Mexican Pacific coast and the Revillagigedo Islands, appear to have important implications in the dynamics of dispersal and thus on the phylogeographic structure of populations.

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**GREAT BARRIER REEF MARINE PARK WHALE AND DOLPHIN CONSERVATION.** (ABSTRACT) In February 2000, the Great Barrier Reef Marine Park Authority finalised a *Whale and Dolphin Conservation Policy* intended to guide management decisions concerning human activities that will, or are likely to, affect the cetacean populations occurring in the Great Barrier Reef Marine Park. The policy focuses on minimising potential adverse effects on cetaceans arising from a variety of human activities, including shipping and boating, deliberate feeding, defence activities, marine construction, coastal development and fishing.

The policy also includes elements relating to management of commercial and recreational whalewatching activities, many of which focus on humpback whales (*Megaptera novaeangliae*). In addition, specific provisions are included for whalewatching activities that involve people swimming, snorkelling, or scuba diving with the animals. Whalewatching can provide people not only with an enjoyable opportunity to observe the animals, but also promote increased understanding of the animals and their needs. Whalewatching operations can provide information on the distribution, relative abundance and behaviour of cetaceans,

which facilitates effective management. However, these benefits must be weighed against the variety of potential adverse effects of this activity, which require careful management in cooperation with the whalewatching industry.

Within the Great Barrier Reef Marine Park, whalewatching activities will be managed through a combination of education, best practices guidelines, codes of conduct, regulations, cetacean refuges and, for commercial tour operations, permits. Whalewatching operations are recognised as a source of important information about the animals, and the potential for the commercial whalewatching industry to become self-regulating is acknowledged.

Copies of the policy may be obtained from GBRMPA or via the website [www.gbrmpa.gov.au](http://www.gbrmpa.gov.au).

Kirstin Dobbs, Great Barrier Reef Marine Park Authority, PO Box 1379, Townsville 4810, Australia (e-mail: [k.dobbs@gbrrmpa.gov.au](mailto:k.dobbs@gbrrmpa.gov.au)); Cheri Recchia, Center for Marine Conservation, 1725 DeSales Street, NW #600, Washington, D.C. 20036, USA; Tony Stokes, Great Barrier Reef Marine Park Authority, PO Box 1379, Townsville 4810, Australia; 29 August 2000.

**WHY HUMPBACK WHALES NEED A SOUTH PACIFIC SANCTUARY.** (ABSTRACT) Humpback whales in the South Pacific have been severely depleted by commercial whaling activities of the past two centuries. Sail whalers of the Nineteenth Century took significant numbers on their South Pacific breeding grounds, but pelagic fleets operating on the feeding grounds of the Southern Ocean during the Twentieth Century grossly over-exploited these populations. New data reveal the extent of the illegal, unreported whaling of past Soviet factory ship operations in the 1950s and 1960s, which were largely focused on the feeding grounds to the south of Polynesia and New Zealand. Since the collapse of the New Zealand whaling industry in 1963, there have been few reports of humpback whales

(*Megaptera novaeangliae*) on their traditional migration routes. Photo-identification studies in Vava'u, Tonga, illustrate how close the Tongan humpback population may have come to extirpation. The same is probably true of all the known breeding grounds in the South Pacific region. The gross, and relatively recent, over-exploitation of the region's humpbacks provides a strong case for protection through a whale sanctuary. Recovering whale populations, which can be best provided for through a sanctuary, would provide valuable economic benefits to the region, and would not threaten fish resources.

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**COMPUTER-ASSISTED MATCHING OF HUMPBACK WHALE PHOTO-IDENTIFICATION PHOTOGRAPHS.** (ABSTRACT) To assist in matching humpback whale (*Megaptera novaeangliae*) identification photographs, a digital image/database system has been developed based on the successful video disc/database system used for Northern Hemisphere humpback whales (Mizroch et al., 1990). Digitally scanned photographs of tail fluke undersides or body flanks are stored in a database as graded images such that a likely group of possible matches is produced when the database is queried. The group of images is viewed to determine whether a match exists. The architecture of the database allows for the easy exchange of just the graded images between research groups for possible matching through storage on CD-ROM discs. From whales photographed off Western Australia, 1990-1998, some 4,000 images of some 2,000 individually-identified animals are currently available. Comparisons within the database and with others, which would have been physically too demanding using earlier manual methods, will now permit

analyses of individual animal life histories and prediction of migratory movements. Suggested strategies and workflow issues for digitisation, long-term image storage, image manipulation software and hardware options are discussed. The system is currently available free from the author ([mailto:elford@mac.com](mailto:mailto:elford@mac.com)) or the Centre for Whale Research (WA) and will be available on the world-wide-web along with a users group.

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## VOCALISATION RATES OF MIGRATING HUMPBACK WHALES OVER 14 YEARS

DOUGLAS H. CATO, ROBERT PATERSON AND PATRICIA PATERSON

Cato, D.H., Paterson, R.A. & Paterson, P. 2001 12 31: Vocalisation rates of migrating humpback whales over 14 years. *Memoirs of the Queensland Museum* 47(2): 481-489. Brisbane. ISSN 0079-8835.

Acoustic monitoring of migrating humpback whales has been carried out since 1981 in conjunction with visual surveys from Point Lookout, Stradbroke Island, on the east coast of Australia. Recordings were made from a drilling boat a few kilometres seaward of the observation point, during the peak of at least one of the annual migration phases. This paper presents an analysis of song vocalisation in relation to the observed movements of the whales to determine the vocalisation rates and their value as an index of relative abundance. The proportion of whales singing as they passed Point Lookout was ~5% during the northern migration (towards the breeding grounds) and ~13% during the southern migration, the difference being statistically significant. There was no significant trend in the proportion of singers as the stock size increased by a factor of 3. From 1982 to 1993, the number of singers passing per 10 hours during the southern migration increased at a rate of 10.6% (95% confidence interval 3% - 19%), consistent with the rate of increase of 11.7% obtained from the visual survey over a similar period. □ *Humpback whales, Megaptera novaeangliae, eastern Australia, vocalisations, song, stock recovery.*

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Sounds of humpback whales, *Megaptera novaeangliae*, have been recorded in the vicinity of Point Lookout on North Stradbroke Island on the east coast of Australia since 1981, usually at the same time as visual observations which have been made there regularly since 1978. This paper compares the acoustic and visual observations from 1981 to 1994. During that period, it is estimated that the number of humpback whales passing Point Lookout increased from ~600 in 1981 to ~2,300 in 1994, based on the stock size estimates and rates of increase from visual observations (Paterson & Paterson, 1989; Paterson et al., 1994).

Point Lookout is particularly suitable for visual observations. Humpback whales passing Point Lookout form the east Australian component of the Area V (130°E - 170°W) population which migrates annually between summer feeding grounds in Antarctic waters and winter breeding grounds inside the Great Barrier Reef (Chittleborough, 1965; Dawbin, 1966). The migration paths converge where the coast extends most eastwards, in the vicinity of Stradbroke I. and Cape Byron. Aerial surveys out to 80km from shore have shown that >95% of humpback whales pass within 10km of Point Lookout, and thus would be within visual range (Bryden, 1985). There have been land-based visual surveys from Point Lookout (Bryden et al., 1990; Paterson &

Paterson, 1984, 1989; Paterson et al., 1994, 2001) and stock parameters and characteristics of the migration are well known.

Humpback whales are particularly vocal, producing both the well known song and 'social sounds' (Payne & McVay, 1971; Winn et al., 1971; Winn & Winn, 1978). The song appears to be related to breeding, possibly as an acoustic display, since the evidence is that singers are males and singing is usually confined to breeding grounds and migration paths to and from these grounds (Payne & McVay, 1971; Winn et al., 1971, 1973; Winn & Winn, 1978; Glockner, 1983; Cato, 1991). A song is a complex and well structured, but stereotyped sequence of themes and phrases of variable duration, but typically averaging ~10 minutes. Individuals may sing for several hours at a time and with the more powerful parts of the song audible for some tens of kilometres in most conditions (Cato, 1991).

This paper presents an estimate of the proportion of whales singing as they passed during migrations, which is of interest in understanding the function of the song, and in using acoustics to estimate abundance. It also tests the effectiveness of an acoustic index as an indicator of relative abundance by estimating the rate of increase of the stock from the numbers of singers passing per 10h in each year's observation period and

comparing this with the result determined from visual observations.

#### MATERIALS AND METHODS

**ACOUSTIC OBSERVATIONS.** These were made using hydrophones suspended from a 4.5m boat, drifting off Point Lookout (Fig. 1). The hydrophone used from 1981 to 1983 was a General Instrument Corporation Z3B on 30m of cable, RAN Research Laboratory designed low noise preamplifiers and a Kudelski Nagra III tape recorder. System response was  $\pm 3$ dB from 20Hz to 17kHz, but it was often necessary to use a high pass filter (-6dB at 55Hz, -20dB at 20Hz) to attenuate the low frequency noise from turbulence. From 1984, Clevite CH17 hydrophones and Sony WMD6 or TCD5M cassette recorders were used, giving a system response from 30Hz to 15kHz, modified by the above filter response when used.

During recordings, the boat was allowed to drift with the current to reduce the noise of turbulence from water flow past the hydrophone. The period of recording was chosen to coincide with the migration peak (late June, early July northbound and late September, early October, southbound) based on the rise and fall of numbers of humpback whales sighted in the region (Chittleborough, 1965; Paterson & Paterson, 1984, 1989; Paterson et al., 1994). Weather conditions were suitable for recording from a small boat on only about half the days over the one to two week observation period. There were two limitations. One was the difficulty of handling the boat in higher sea states and keeping the recording equipment dry and operational. The other was that higher wind speeds substantially increased background noise and substantially reduced distances that singers were audible. This limited effective recording to wind speeds of <20 knots. Limitations on opportunities to record at sea, and the small stock size in the earlier years limited the size of the sample, particularly the number of singers.

Bryden (1985) reported the distribution of humpback whales in the vicinity of Stradbroke I. based on aerial surveys from shore to 70km seaward of Point Lookout. He found that >95% of whales passed within 10km of the headland and >70% within 5km. Generally the position of the boat was within this 5km wide east west strip. Water depths where most whales pass Point Lookout increased with distance seaward from 20-90m and the boat was usually in depths of 30-50m.

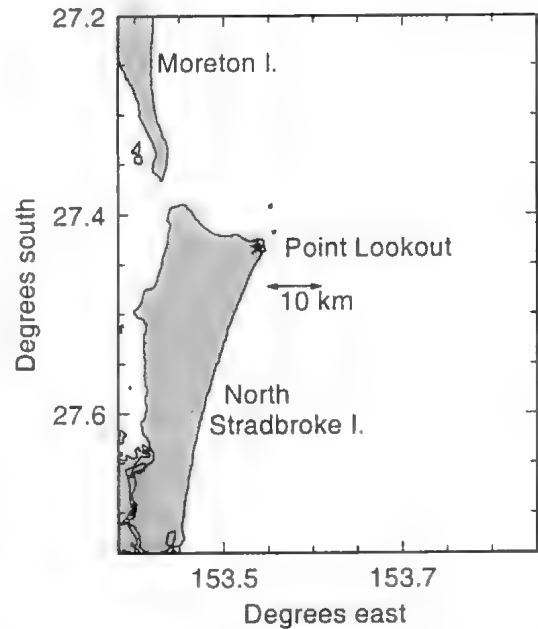


FIG. 1. Map showing the location of visual observation position on Point Lookout. Acoustic observations were made from a boat drifting a few kilometres seaward.

Analysis of the received sound signal levels and system calibration were made using a Brüel and Kjær Digital Frequency Analyser type 2131 and Hewlett-Packard 3582A analyser.

**VISUAL OBSERVATIONS.** These were made each year from the same 67m high position at Point Lookout (Fig. 1) and the methods conformed with surveys dating from 1978, described by Paterson et al. (1994). A continuous watch was maintained during daylight for each day of the observation period in the earlier years of this study, and on three to four days per week over a longer period during the later years. Visual observation covered a larger part of the migration period than the acoustic observations. While we attempted to ensure that visual and acoustic observations were concurrent, this was not always possible. The area of ocean within visible range covered a sector between true bearings of 030° and 120° and extending to about 10km from shore under typical conditions. The boat was allowed to drift within this sector and was usually 3-5km seaward of the headland, though on some occasions it was out of sight. Humpback whales passing through the sector were usually seen a number of times and depending on their positions, paths taken and sighting conditions were

TABLE 1. Summary of the data.

	Northern migration	Southern migration
Years of acoustic data	1984, 1989-91, 1994	1981-89, 1992, 1993
Years of concurrent acoustic and visual data	1984, 1989-91, 1994	1981-85, 1987, 1991, 1992
No. of days acoustic data		
Total all years	26	44
Yearly range, average	3 - 7, 5.2	2 - 5, 4.0
No. of hours acoustic data		
Total all years	145.9	247.4
Yearly range, average	18.0 - 46.1, 29.2	10.1 - 36.7, 22.5
No. of hours of concurrent acoustic and visual observations	118.9	159.9

visible for <1h to >5h. Table 1 summarises the data for all acoustic observations and for those taken concurrently with visual observations.

#### BASIS FOR THE ACOUSTICS ANALYSIS

**THE EFFECT OF THE OCEAN ENVIRONMENT ON AUDIBILITY OF SINGERS.** The distance over which a source in the ocean is audible (by ear) or detectable (by instrumentation) varies widely because of variation in ocean conditions. The limiting range of detection depends on the source level (power generated by the source), the propagation loss as sound travels to the receiver, and the background noise against which the signal must be detected. The received sound signal will be detected or heard if the signal to noise ratio exceeds a certain threshold value.

Sound travels to much greater distances in the ocean than it does in the atmosphere because the absorption attenuation, the loss of energy from the sound wave, is much lower. Propagation in shallow water (<200m) involves many reflections from the sea surface and the bottom. While surface reflection occurs with little loss, reflection from the bottom may involve significant energy loss which varies widely for different bottom materials. Consequently propagation loss varies widely from one shallow water site to another. Temporal variability depends on variation in the sound speed-depth profile and this depends on the mixing of the water by surface waves and currents. Surface wave action tends to mix the water and minimise this variability, as was the case in the study area where significant wind and wave action is usual. The variability of propagation loss can be minimised in shallow water by confining the work to a fixed location, as in this study. Shoals and reefs tend to block the propagation of sound and need to be avoided and

we usually positioned the boat to have clear path to passing whales.

There is a general ambient or background noise in the ocean due to contributions from many physical and biological sources of sound. The good propagation of sound allows contributions from sources at much greater distances than in the atmosphere so the noise level is high and variable. Ambient noise in Australian coastal waters varies by more than 20dB mainly as a result of variations in wind speed and biological activity (Cato, 1997). Breaking waves generate high noise levels which are directly related to wind speed (and less to the actual wave height or sea state, Wenz, 1962). Fish and invertebrates, such as snapping shrimps (Everest et al., 1948) also produce high noise levels, which vary temporally with diurnal and other variations in behaviour, and spatially with habitat variation (McCauley & Cato, 2000). The effect of an increase of 20dB in ambient noise is to reduce the amount of propagation loss that can be tolerated at the threshold of detection by 20dB. In free field propagation, this corresponds to a factor of 10 in distance, more if the sea floor is highly reflective or less if it is highly absorptive. Consequently the typical variation of ambient noise in coastal waters causes the distance of audibility to vary by a factor of ~10. The consequent variation in the area over which singers are audible would be a factor of ~100, since the area depends on the square of the distance. Thus simply counting the number of singers audible is of little value in estimating stock parameters, unless the effects of ambient noise and sound propagation are accounted for.

The effect of ambient noise can be removed by measuring the level of the received signal, since this equals the difference between source level and propagation loss, and is thus independent of ambient noise. This requires the received signal to noise ratio to be above the threshold of detection, but the high source levels of whale sounds means that this would normally be the case for sources at distances of kilometres to tens of kilometres. If the source level and propagation loss are known, the distance to each source can be calculated.

Our perception of the loudness of a sound received underwater is of almost no value in estimating the received level, since this depends on the signal to noise ratio. We hear the sounds through headphones or a loudspeaker so our only criterion for judging the loudness of the signal in absolute terms is to compare it with the



background noise. The wide variation in ambient noise causes wide variation in apparent loudness, and for the same loudness, singer distances vary as ambient noise varies. This may be counter intuitive but results because the decrease in received signal level with distance in the ocean, even to distances of tens of kilometres, is far more gradual than the decrease with distance in air. A doubling of the distance results in only a small change in received level, much smaller than the variation of ambient noise.

**APPLICATION OF ACOUSTICS TO STOCK ASSESSMENT.** An estimate of the abundance of a whale stock usually involves sampling the spatial or temporal density of individuals and scaling the results up to the full spatial or temporal extent of the stock. For example, for a stock that is resident in an area, samples of the spatial density are made and the result then scaled up to the total area. Off east Australia the stock is migrating and as most whales pass within visual range of headlands such as Point Lookout, the approach has been to sample the temporal density by counting the number of whales passing per 10-h day on the basis that any individual would pass through the area only once in a migration. The result is then scaled up to the total period of migration (see for example, Bryden et al., 1990; Paterson et al., 1994).

The use of acoustic observations to determine spatial densities requires an estimate of the distances to singers so that only those within the area of the sample unit are counted. In temporal sampling, it is also necessary to estimate the distances of singers to ensure that they are close enough to pass the observation point within the sampling period, since singers may be audible for tens of kilometres. The most accurate way of determining distances is to use an array of three or more accurately positioned hydrophones, which also allows sources to be localised and their movements tracked from the differences in times of arrival of signals to the different hydrophones. Some examples of this method applied to locate baleen whales are given by Cummings & Holliday (1985) and Clark, Ellison & Beeman (1986) for bowhead whales, *Balaena mysticetus*, and Frankel et al. (1995) for humpback whales (see Noad & Cato, 2001, for further discussion and application to the east Australian humpback whale migration). This method is logistically complicated and requires substantial analysis effort.

Simpler methods of estimating distances may be more attractive for routine surveys because of

lower cost and effort, but are less accurate and will result in greater errors through variability in source levels and propagation loss. Little data on variation of source levels of baleen whale sounds are available, though significant variation has been observed for bowhead whales (Cummings & Holliday, 1987) and finback whales, *Balaenoptera physalus*, (Watkins et al., 1987).

In the present study, determination of the proportion of passing humpback whales that were singing was made by comparing the concurrent acoustic and visual observations. If a singer was audible, it was necessary to establish that it was one of the whales seen passing and not a more distant whale. This was done by measuring the received level of the sounds and estimating the distance of the source based on estimates of source level and propagation loss. In many cases it was not possible to identify the particular whale that was singing because of the uncertainties of the estimate, but it was possible to establish that the singer was among the visually-observed passing whales. Only the most intense sounds of the song, usually low frequency moan-like sounds were used to determine if a singer was one of the visually observed whales. These sounds are considered to be the most consistent for this purpose, in that they tend to persist with less yearly change and they also provide the best signal to noise ratios.

Where the singer could be identified unambiguously, it was possible to make an estimate of the source levels of the sounds. Propagation loss was estimated using the semi-empirical expressions of Marsh & Schulkin (1962) for shallow water. At the short distances at which these estimates were made (usually within 300 m, a few times the water depth) this should be reliable. Measured broad band mean square source levels varied from 176–185dB re 1µPa at 1m. Some of the variation is due to variation between the different sound types but there would be a significant uncertainty due to errors in estimating the distance to the source (which was done by eye). The results are, however, consistent with the range of 175–188dB re 1µPa at 1m reported by Winn et al. (1971) and the mean measured in a 300Hz band by Frankel (1994) of 174dB re 1µPa.

From the received level, an estimate was made of the range of possible distances of a singer given the variation in source level and uncertainty in propagation loss. This was then compared with the positions of whales observed visually.

Singers were usually audible for several song cycles, often for more than an hour, allowing a number of different estimates as positions of the whales and singer changed. When the singer was closest, the uncertainty in its position was least.

A different approach was used in determining an index of relative abundance to test the effectiveness of acoustics in estimating the annual rate of change of stock size. Since this has potential application for situations where there are no visual observations, there was an advantage in developing an index that was independent of visual observations. The index chosen was a count of the number of singers passing per 10h listening, averaged over the total listening period for each year. The criterion used to establish that a singer heard was passing was that it passed within 5km of the boat, based on the received level of the sounds, the propagation loss and source level. This covered a 10km-diameter circle centred on the boat drifting a few kilometres from shore, and was chosen to match approximately the 10km wide strip of the visual observations. An error in the estimate of propagation loss would change the size of this circle, but since this would be consistent from year to year, the error would not affect the value of the criterion as a relative index of abundance. There remains some uncertainty due to possible variations in source level. Because singers were audible for long periods, minimum estimated distances were usually significantly <5km, reducing uncertainty in the results. All acoustic data were used in this analysis, irrespective of whether there were visual observations during the same period, while the estimate of the proportion of whales singing was confined to data that were concurrent with the visual observations.

## RESULTS

**PROPORTION OF HUMPBACK WHALES SINGING.** Table 2 compares the total numbers of singers passing with the total numbers of humpback whales passing during the periods of concurrent acoustic and visual observations. An average of ~5% of passing whales were singing on the northern migration and 12% on the southern migration. A Chi squared test (Siegel & Castellan, 1988) showed that the difference in the results for the two migrations was significant ( $P < 0.05$ ). Figure 2 shows results for the southern migration as a plot of the number of singers in each year versus the number of whales passing. There is a good correlation between numbers of singers and total numbers of whales passing

TABLE 2. Number of singers passing compared with total numbers of whales passing Point Lookout.

	Northern migration	Southern migration
Years of observations	1984, 1989-91, 1994	1981-85, 1987, 1992, 1993
Hours of observation	118.9h	156.7h
Singers passing, total	8	27
Singers passing when concurrent acoustic and visual observations	7	12
All whales passing, total	141	114
All whales passing when concurrent acoustic and visual observations	141	100
Proportion singing (range of results for each year) from totals	0.05 (0.028 - 0.083)	0.12 (0.083 - 0.130)

(correlation coefficient 0.989) and the slope of the linear regression line on the data provides another measure of the proportion of whales singing. The slope of 0.132 (95% confidence interval 0.105-0.160 %), gives a value of 13.2% ( $\pm 2.8\%$ ) for the proportion of whales singing, consistent with the proportion obtained from the total numbers of singers and whales. The number of singers versus whales passing during the northern migration is shown in Fig. 3. The spread of data for the northern migration is too small to obtain meaningful regression of singers on total whales.

Tyack (1981) found that out of 129 humpback whales observed in the Hawaiian breeding grounds, 21 were singing, a proportion of 16.3%. A Chi square test (with correction for continuity) did not show a statistically significant difference

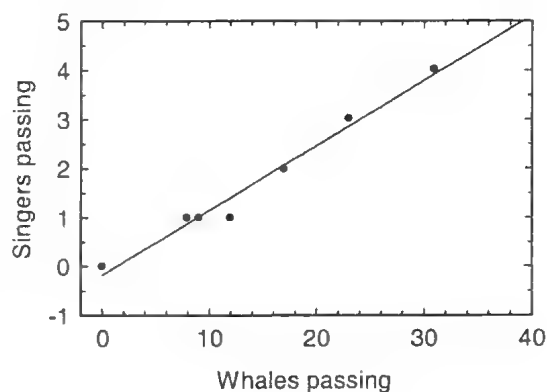


FIG. 2. Relationship between the number of singers and the total number of whales passing Point Lookout, at the peak of the southern migration each year (1982-1989, 1992).

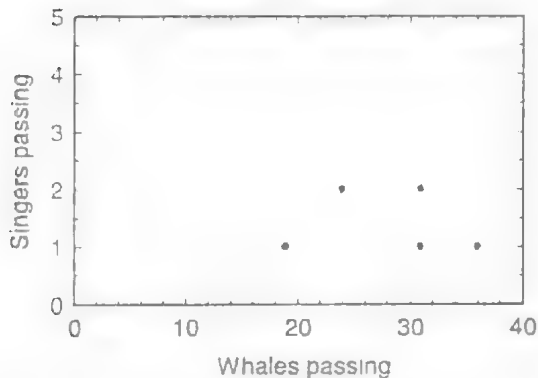


FIG. 3. Relationship between the number of singers and the total number of whales passing Point Lookout at the peak of the northern migration each year (1984, 1989, 1990, 1991, 1994).

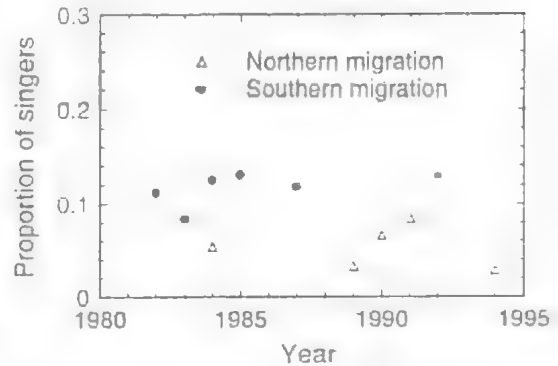


FIG. 4. Proportion of whales singing as they passed Point Lookout for each year of observation at the peaks of the northern and southern migrations.

between the Hawaiian result and the east Australian southern migration result ( $P < 0.5$ ).

Figure 4 shows the year by year proportion of singers passing from 1982 to 1994. Little consistent trend with year is evident in the data for either migration, within the spread of the data.

**ACOUSTIC INDEX OF RELATIVE ABUNDANCE.** Figure 5 shows the average number of singers passing per 10h for each year of observations during the southern migration. A logarithmic scale is used for the number of singers so that a constant rate of increase (or exponential increase) would appear as a straight line. The results show an increase over the years, though there is significant spread of data. A linear regression line was calculated for the logarithm of singers per 10h versus the year of observation to obtain the best estimate of a constant rate of increase. This gave a rate of increase of 10.6% with a 95% confidence interval of 3.1-8.6% and correlation coefficient of 0.76. This result, for the period 1982 to 1993 is consistent with the rate of increase of 11.7% (95% confidence interval 9.6-13.8%) obtained from visual observations from Point Lookout from 1984 to 1992 (Paterson et al., 1994), though the confidence interval is much wider for the acoustic result. The acoustic observation sample represent a much smaller number of individuals, partly because only a proportion of the passing whales was singing and partly because of the shorter period of observation in the acoustic survey. The number of singers in a year varied from 1 to 6 so the spread in the data in Fig. 5 is to be expected, and such a small number of individuals limits the reliability of the sample.

In an attempt to improve the sample size, numbers of singers per 10h were pooled in two year blocks and the results are shown in Fig. 6. The result shows less spread of data and the regression line gives a rate of increase of 12.4% with 95% confidence interval of 10.9-13.9%, within the range obtained from visual observations. This result suggests that a longer period of observation with the detection of more singers would have been appropriate for the purpose of estimating relative abundance.

Data for the northern migration were considered insufficient to obtain a reliable estimate of the rate of increase in stock size, with fewer years and smaller proportion of singers than for the southern migration.

## DISCUSSION

Although sample sizes were small when measured in terms of the numbers of singers passing Point Lookout, the results do show consistency.

Humpback whale singing is considered to be related to breeding. It is usually observed on the breeding grounds and on migration to and from the breeding grounds (Payne & McVay, 1971; Winn et al., 1971; Winn & Winn, 1978; Cato, 1991), but is rare in higher latitudes where most feeding occurs. While the proportion of whales singing on the southern migration off Stradbroke I. is significantly higher than that for the northern migration, it is consistent with that observed on the Hawaiian breeding grounds. There is no apparent environmental difference off Point Lookout between the two migrations. Monthly averages of water temperatures differ by  $<1^{\circ}\text{C}$  between the times of the two migrations

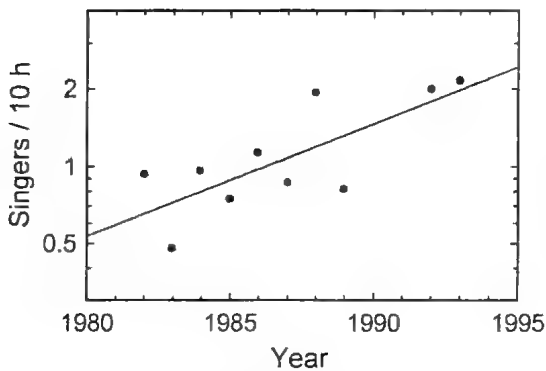


FIG. 5. Number of singers passing Point Lookout per 10h at the peak of the southern migration in each year of observation.

(Paterson, 1986), less than the variation observed in measurements from the boat within a migration period. While there is evidence that singing is confined to mature males (Winn et al., 1973; Glockner, 1983), the proportion of mature males passing at the times of recording is similar for the two migrations (Chittleborough, 1965; Dawbin, 1997). This suggests that the whales are closer to breeding condition on the southern migration, moving away from the breeding grounds than they are on the northern migration, when approaching the breeding grounds. Humpback whales are clearly in transit as they pass Point Lookout — whales pass through the observation area with relatively little deviation and only occasional significant interaction. The southern migration, however, shows more meandering and surface interaction than the northern migration, and if this is interpreted as behaviour indicative of the breeding areas, this is consistent with the increased proportion of whales singing during the southern migration. There is, however, greater similarity in behaviour between the two migrations, than there is between that on the southern migration and on the Hawaiian breeding grounds.

The humpback whale stock passing Point Lookout is estimated to have increased from ~600 in 1981 to ~2,300 in 1994 (Paterson & Paterson, 1989; Paterson et al., 1994). Over the period of the southern migration data it varied from ~660 in 1982 to ~2,100 in 1993, a factor of >3. The migration has remained consistent over this period, based on the lack of apparent change in its timing, the rate of rise and fall in numbers passing over the course of the migration and the consistency in the proportion of the stock passing

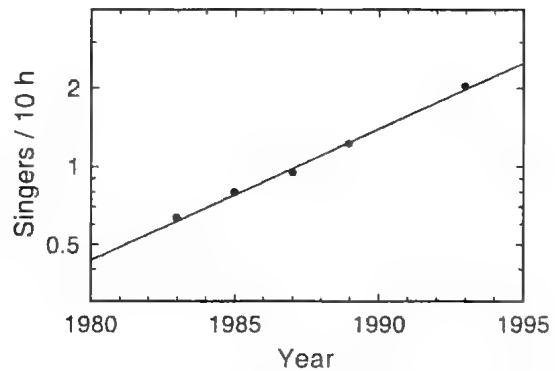


FIG. 6. Numbers of singers passing Point Lookout per 10h at the peak of the southern migration — data pooled in two-year blocks. Point shown for each year is the data pooled for that year and the previous year.

in 4, 8 and 10 weeks at the peak in 1987, 1992 and 1999 (Paterson et al., 1994, 2001). Thus the spatial and temporal separation of the migrating humpback whales can be expected to be inversely proportional to the stock size, i.e. to have decreased by a factor of >3 from 1982 to 1993. In 1982, the average temporal separation between groups of whales passing during the four weeks at the peak of the southern migration would have been ~4.9h (based on an average group size of 2.17, Paterson et al., 2001) and the average separation of singers would have been ~17h. Using the estimates of migration speed of Dawbin (1966) (~1.5 knots for long-term movement of stock) and Chittleborough (1965) (mean of 3.4 knots from aerial observations), the average separation of groups would have been from 13.6–39km and the average separation of singers 47–136km. This raises the question of how changes in the song are communicated over large distances, given the separation of whales. In 1983 and 1984, songs recorded within a few weeks at locations separated by thousands of kilometres along the east coast of Australia were similar, even though the song was changing (Cato, 1991).

The lack of significant trend to a change in the proportion of whales singing over the period when the stock size increased by a factor of three, suggests that singing is not driven by the density or proximity of singers or non singers. In the early years of our observations it was very unusual to hear more than one singer at a time whereas in the later years, two or more were usually audible. Difference in the proportion of whales singing between the two migrations also suggests that

singing is internally driven. In a captive female leopard seal, production of intense song-like sounds was highly correlated with hormonal changes related to breeding (Rogers et al., 1996). If production of song is driven by hormonal changes, this would be independent of the density and proximity of singers and non singers, and would also be consistent with a higher proportion of singers when behaviour is more indicative of breeding as on the southern migration.

These considerations also support the view that the humpback whale song is an acoustic display associated with breeding. The lack of dependence of song production on separation of singers and non singers suggests that the singing is not interactive or agonistic communication between individuals. Although the song is complex and contains a large number of sound units of different kinds, it is very stereotyped. Since information is carried only in variations in the stereotype (Cato, 1991), most of the potential to carry information is not used and this further supports the idea of the song as an elaborate acoustic display.

Extensive data concerning east Australian humpback whale population parameters have been obtained from long-term visual observations at Point Lookout. Stock size and rate of increase are well established. The similarity of the rate of increase in stock size estimated from the acoustic data to that estimated from visual observations, indicates that acoustics may be useful in estimating relative abundance with simple recording systems in areas where visual observations are more difficult to conduct effectively.

#### ACKNOWLEDGEMENTS

We thank Dr John Quayle for providing the boat and his participation in the recordings off Stradbroke I. in 1981 and 1982 and Les Nash for providing the boat and technical assistance from 1983.

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# **GEOGRAPHIC AND TEMPORAL VARIATION IN AREA V HUMPBACK WHALE SONG. (ABSTRACT)**

Much of the background information on humpback whale song structure comes from the Northern Hemisphere, where populations are localised on mating and calving grounds. Breeding sites for the Southern Hemisphere Area V population of humpback whales have not been identified, however their migration takes them close to the coast, enabling researchers to gain insight into song evolution over

hundreds of kilometres prior to and following visiting the breeding grounds. This paper discusses song collected during the years of 1986, 1991 and 1993 from various locations along the east coast of Australia, examining the influence of latitude and season on song structure during migration.

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# **ASSOCIATIONS AMONG HUMPBACK WHALES AT THE ARCHIPIÉLAGO REVILLAGIGEDO, PACIFICO MEXICANO, 1996-2000. (ABSTRACT)**

Since 1986 photographic identification studies of the humpback whales (*Megaptera novaeangliae*) wintering among the Archipiélago Revillagigedo have demonstrated a consistently high resighting rate of individuals within and between years (40-50%). In 1996, we began a long-term study of this population taking advantage of these unusual resighting rates to acquire detailed behavioral data on many individuals. We investigated patterns of association among the 631 individuals sighted in 1996-1999 by searching the sighting database for all pairs of whales sighted together in more than one group. Although the vast majority of whales associated only one time in four years, 142 pairs were seen together 2-7 times, and 11 pairs associated in more than one year. Recurrent associations often occurred in small groups (duos, trios, cow/calf with escort), whereas associations in competitive groups seldom recurred. Among the limited sample of known-sex pairs, male-male associations were most prevalent and recurred most frequently. There were

seven male-male pairs that were sighted together both as duos and in competitive groups, two of which were sighted together in multiple years. These observations give additional support to the idea that some males may form coalitions. These analyses will improve as we add more years of behavioral observations, and determine the sex of more individuals by behavior and by genetic analysis of biopsy skin samples, which also will allow us to test the relatedness of associates. We also plan to test the randomness of these associations.

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# **WHALE-WATCHING IN NEW CALEDONIA: A NEW INDUSTRY. (POSTER)**

Commercial whale watching cruises began in 1995. At that time 3 tourist operators completed only a few day cruises during the entire season from July to September. Since that time this commercial activity has grown. In 1999, 141 cruises were realised by 19 boats for more than 1,984 persons mainly originating from New Caledonia. The direct economic value has reached 13 million FCFP.

The activity of whale watching is limited to one species: the humpback whale (*Megaptera novaeangliae*) which migrates to New Caledonia in winter to breed. This activity is located in the southern part of the lagoon close to a sheltered bay, overhung by terrestrial observational points, in an area that presents a rich and well preserved natural marine and terrestrial environment favourable to the development of ecotourism.

The success of sighting whales varied from 50-80%. Consequently whalewatching is often associated with other activities, like sailing or scuba-diving, so as to be more attractive to tourists.

Guidelines on 'how to approach the whales' have been published in 1999 by the Province South, but New Caledonia currently lacks any policy or management plan concerning humpback whales within its territorial waters and perhaps more importantly, there is a complete absence of legislation concerning cetaceans in New Caledonia. Issues that need to be addressed are the present uncontrolled development of the whalewatching industry and the impact of human activities on the well-being of the local humpback whale population (e.g. pollution and maritime traffic).

Claire Garrigue & Sabrina Virly, Opération cétacés BP 12827, Nouméa, New Calédonia (e-mail: op.cetaces@offratel.nc); 29 August 2000.



## REFLECTIONS OF AN ACOUSTICIAN

A.C. KIBBLEWHITE

Kibblewhite, A.C. 2001 12 31: Reflections of an acoustician. *Memoirs of the Queensland Museum* 47(2): 491-498. Brisbane. ISSN 0079-8835.

In the early 1950s a fixed hydrophone array was set up off the coast of New Zealand. The local ocean environment is characterised by a complex oceanographic structure, but there was confident expectation that this installation would help provide an understanding of the phenomena involved in the propagation of low-frequency sound in local conditions. Some of the surprises experienced in this examination of the acoustic properties of the ocean, including a report of the first probable acoustic encounter with the humpback whale in the Southern Hemisphere, are described in this personal account. □ *New Zealand, marine environment, acoustic properties, humpback whale song.*

A.C. Kibblewhite, Department of Physics, University of Auckland, Private Bag 92019, Auckland, New Zealand; 28 May 2001.

The submarine almost won World War II for Germany (Ruge, 1957). That the allies eventually achieved superiority in the Battle of the Atlantic was due largely to the development of radar and its joint deployment with sonar (Kemp, 1957). Both systems involve the transmission of a directional pulse of energy (electromagnetic in the case of radar and acoustic in that of sonar) and the detection of any echo returned by an illuminated target.

On typical anti-submarine warfare vessels of the time, the sonar operated ca. 10-20kHz, used transducers of about 1m in diameter, and achieved detection ranges of about 10km. It was well known at the time that the attenuation of sound in the ocean decreased almost linearly with the frequency of the sound used and that improved performance should be achieved at lower frequencies. However, if the frequency was reduced to achieve a longer detection range, the transducer size had to increase to achieve comparable directionality, so that engineering problems severely constrained the use of lower frequencies in ship-borne sonars.

In the post-war period interest switched from 'active' to 'passive' systems, in which the aim was to detect and locate the self-noise generated by an underwater source (like a submarine), rather than an echo produced by reflected radiation. Such an approach could potentially exploit the thousand-fold decrease in attenuation that results when the acoustic frequency of interest is reduced from 10,000Hz to 100Hz. But any such change called for a better understanding of the factors influencing long-range transmission in the ocean and its ambient noise. These requirements led to the introduction of a new

branch of naval science into the defence organisations of many countries, including Australia and New Zealand. As with many branches of oceanography, the propagation of sound in the sea and its noise have been of importance to whale studies. Significant contributions have arisen from many activities, including those in Australia (Cato, 1991; Hunter, 1996). This account deals with some of the early experiences in New Zealand.

### PROPAGATION STUDIES

**DETECTION OF OCEANOGRAPHIC FRONTS.** In an experiment for evaluating the propagation properties of the ocean, a hydrophone is deployed from a receiving ship while another ship (or an aircraft) drops sound signals as it opens range. Such a procedure was used to establish the factors controlling propagation in New Zealand's continental waters and to investigate any seasonal variation that occurred. On other occasions New Zealand's unique position in the Southern Ocean allowed examination of longer oceanic paths.

One of the first of these experiments involved propagation across the Tasman Sea (Kibblewhite & Denham, 1967). An aircraft dropped explosives as it flew towards Australia and the signals were received on a hydrophone laid off the southern fiords of west New Zealand. Amongst other information, the experiment demonstrated for the first time that oceanographic fronts, like the Subtropical Convergence, could be identified and positioned acoustically by the change in transmission characteristics observed as the source moved from one water mass to another. The trial also demonstrated, in a very effective way, the difference between the

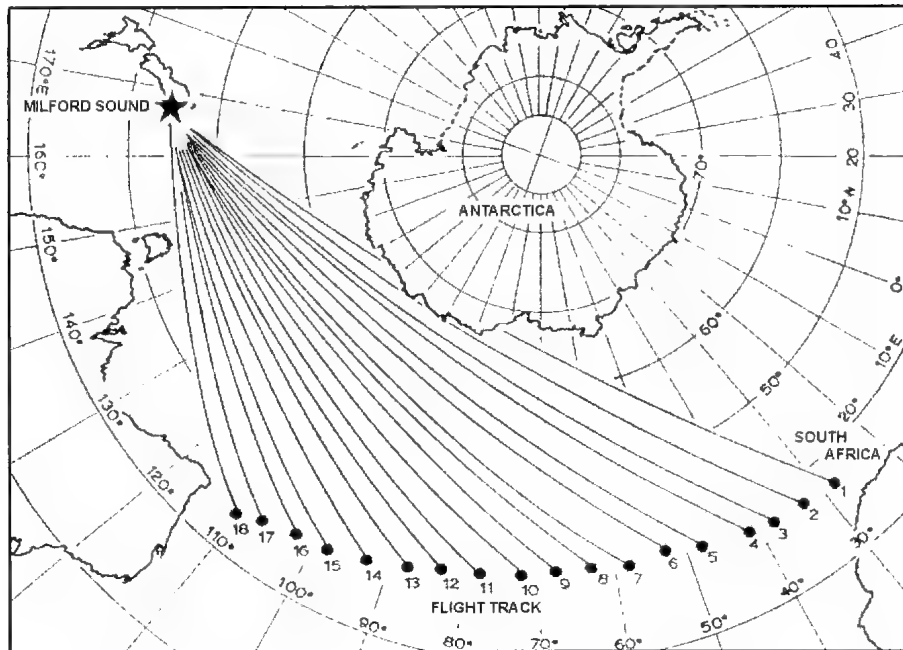


FIG. 1. Project Neptune, Southern Ocean transmission paths.

speed of sound in water and that of electromagnetic radiation in the atmosphere. After the pilot's last 'bomb's away' message on the radio there was a delay of nearly 20 minutes before the sound of the detonation reached us in New Zealand, approximately 1,800km away. Other acoustic experiments have subsequently demonstrated the presence of similar fronts in other oceans (Kibblewhite & Browning, 1978).

**PROJECT NEPTUNE.** Transmission paths of even greater length were involved in Project Neptune. In this experiment an aircraft of the US Airforce dropped sound signals along the two legs of a flight path from Bermuda to Capetown and Capetown to Perth. Recordings of the resulting acoustic signals were made in New Zealand during the second leg of the flight (Kibblewhite, Denham & Barker, 1965). The transmission path for the most distant of the signals received was approximately 10,000km, nearly one quarter of the Earth's circumference. In spite of the distances involved, the results demonstrated that a propagation path existed through the Southern Ocean, provided the great circle path between source and receiver was clear of intervening topography (Fig. 1). In all cases the signal character was consistent with the travel path passing through at least three different water masses. The results provided, however, further

confirmation of the remarkable effectiveness of the deep ocean in transmitting low-frequency sound.

**CHASE V.** In the 1960s the difficulty of distinguishing between a natural seismic event and a covert nuclear explosion presented a serious impediment to the negotiation of a nuclear test-ban treaty. The Chase V experiment was designed to help resolve these difficulties by monitoring the seismic and acoustic signals produced by a large underwater explosion. In this project an old Liberty ship containing 1,000 tons of TNT was scuttled at a specific location off Cape Mendocino and set to explode at the depth of the SOFAR channel axis (Fig. 2). Our participation involved monitoring any signals which might reach New Zealand (Kibblewhite & Denham, 1969).

It transpired that, not only was a direct arrival observed, but another hour went by before reverberations from topography throughout the Pacific Ocean gradually died away. The first arrival, which took 90 minutes to cross the Pacific, confirmed that a direct water path from Cape Mendocino to New Zealand existed, in spite of the extensive intervening topography. The length of the transmission path was again nearly one quarter of the Earth's circumference.

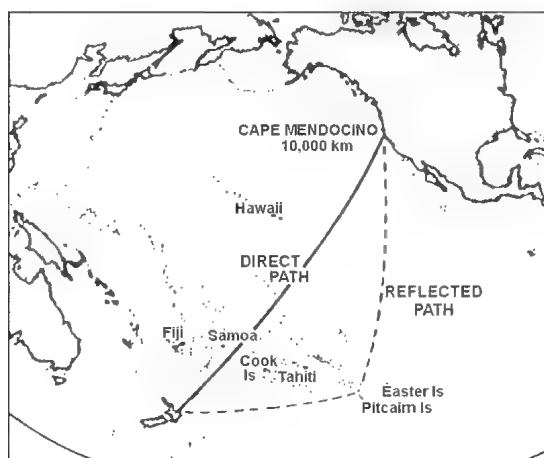


FIG. 2. CHASE V, transmission paths.

Six major echoes in the reverberation following the main arrival were particularly striking. These signals were subsequently identified with reflections from Henderson and Pitcairn Islands, and large underwater mountains on the Tuamotu Ridge which were undiscovered at the time (Kibblewhite & Denham, 1971).

This evidence of a direct acoustic path from North America to New Zealand, together with the evidence from Project Neptune, pointed to the possibility that a deep-water path might exist from the west to the east coasts of the North American mainland, a distance of nearly half the Earth's circumference.

#### AMBIENT SEA NOISE

**HUMPBACK WHALE SONG.** Whatever the propagation conditions encountered (and it is apparent that they can be very favourable at low frequencies), the successful detection and location of an acoustic source by passive techniques will depend ultimately on the relative strengths of the signal generated by the source and the local sea noise at the listening site. Ambient sea noise is thus as critical as propagation in the successful application of underwater sound. Because a proper understanding of any geophysical process requires long-term study, it was decided to base investigations of this parameter on a fixed, semi-permanent hydrophone installation, located off Great Barrier Island (Fig. 3).

Preparation for the installation of this facility extended over a year. A large sum of money was committed to the purchase of armoured cable, the commissioning of a cable ship to lay the cables, construction of large underwater tripods,

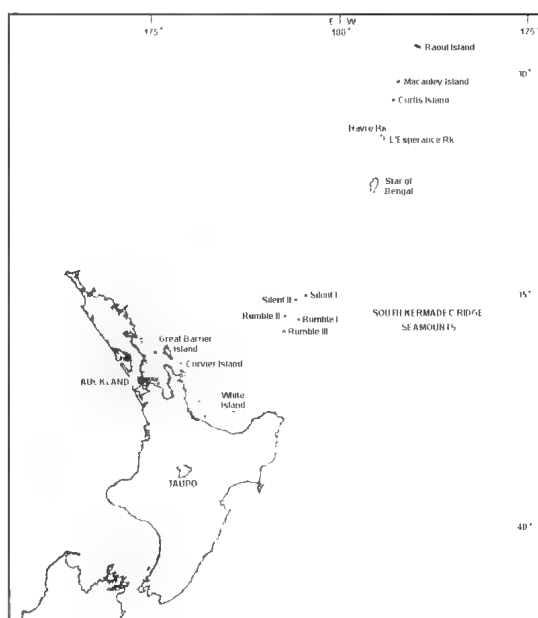


FIG. 3. Great Barrier Island, the Taupo-White Island-Raoul Island volcanic zone and the South Kermadec Ridge seamounts.

purchase of land, construction of a laboratory and living quarters on an isolated island, a training course to acclimatise divers for work in the water depths involved and even the purchase of Model 3 of the first television camera employed in underwater exploration (which was built to support the search for the Comet aircraft that crashed in the Mediterranean about that time). Further, the deployment was not completed without drama. There were ship strikes, cables became wrapped around ship's screws and near groundings resulted, divers collapsed underwater and the hours at sea were long and exacting.

However, the time finally came to connect the underwater array to the shore electronics, albeit in temporary accommodation. A few of us were working late on a cold night to achieve this. We could well have waited till the morning but curiosity drove us on. We did not know exactly what to expect but were smugly confident that we would be listening in to one of the quietest environments in the ocean. Instead we were 'blasted' by some biological community in full song. Our expectations of the hoped for 'silent sea' were certainly not fulfilled.

As it turned out we were unknowingly eavesdropping on migrating humpback whales. This activity, dubbed by the staff as the 'Barnyard

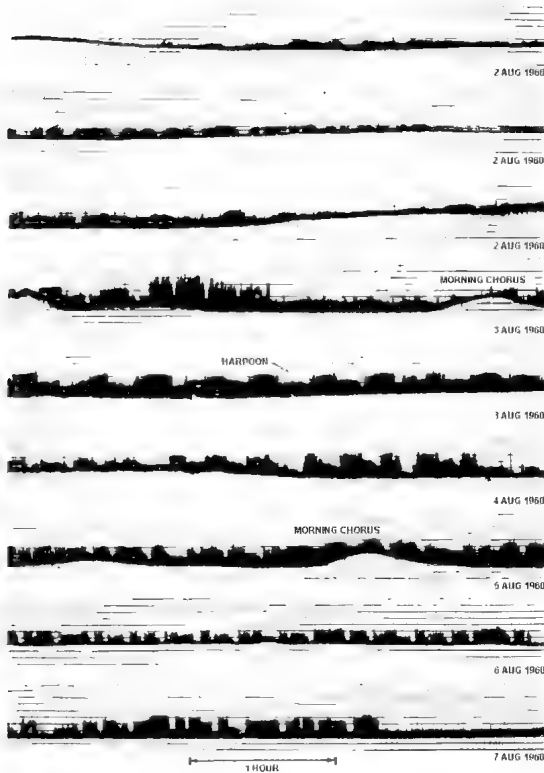


FIG. 4. Humpback whale song recorded off Great Barrier Island 1960.

Chorus', could persist for days at a time (Fig. 4). It was most marked between June to December, during the annual migration. Incidence declined to low levels after 1961, no doubt due to the impact of a local whaling operation (Dawbin, 1967).

Two features of this early encounter are noteworthy. First, the apparent disregard of the whales to the harpoon that was routinely fired in their midst during this period (Fig. 4, 2 August 1960) and second, the activity encountered was probably the first acoustic experience of humpback whale song in the Southern Hemisphere (Kibblewhite et al., 1967).

**OTHER BIOLOGICAL SOURCES.** Signals from other biological sources were observed, although less frequently, at several sites around New Zealand. These signals were too low in frequency to be recorded satisfactorily by the tape recorders then available. However typical features could be established (Kibblewhite et al., 1967).

**20-second Pulse.** The '20-second pulse' was so named by virtue of its pulse length. The spectrogram (line a) at the top of Fig. 5 and the higher speed presentation at the bottom of this figure (line f) show the pulse as a function of frequency and time. The 1/3 octave analysis given in lines (b) and (c) show the pulse is an almost pure tone of about 23Hz. Record (d) indicates the regularity and spacing of a pulse sequence. (The 1/3 octave resolution of these early spectra was the best achievable before computers gave us access to modern spectral analysis.)

**5-second Pulse.** The '5-second pulse' was similar in character but shorter in length and not so pure in tone. The dominant frequency was again around 25Hz. Pulses of similar type were also observed at other sites around New Zealand, and a call-answer sequence was often observed. The signals were attributed to whales but no particular species was identified. Even so these observations of long, low-frequency pulses in the South Pacific were reassuring to the acousticians in the Northern Hemisphere as they confirmed that the pulses were a worldwide phenomena and not necessarily a new weapon of the cold war. Examples are given in figs 4, 5 and 6 of Kibblewhite et al. (1967).

**Significance of the 25Hz Band.** The 25Hz band, in which many whale calls operate, coincides with that at which the attenuation of sound in the deep ocean is a minimum (Kibblewhite & Hampton, 1980). Given optimum propagation conditions, whale calls of this type could therefore be expected to travel long distances. In our early experiments we estimated source levels of the above pulses were about 50Pa/Hz at one metre. Using expected spreading and attenuation rates for deep water, we then estimated that measurable signals might prevail at distances of several thousand kilometres. Speculative as this was at the time, the US Navy has recently reported tracking a particular whale for several weeks as it moved along the European coast and that they did this from a SOSSUS station on the other side of the Atlantic. If whale hearing is as good as ours, they have a remarkable communication system.

Further evidence of the long distances whale signals can travel is provided by the comparison of the spectra of Fig. 6, which were recorded in the North and South Pacific Oceans (Kibblewhite et al., 1976). The northern spectrum was recorded by a hydrophone moored in deep water in the middle of the Pacific, with excellent propagation

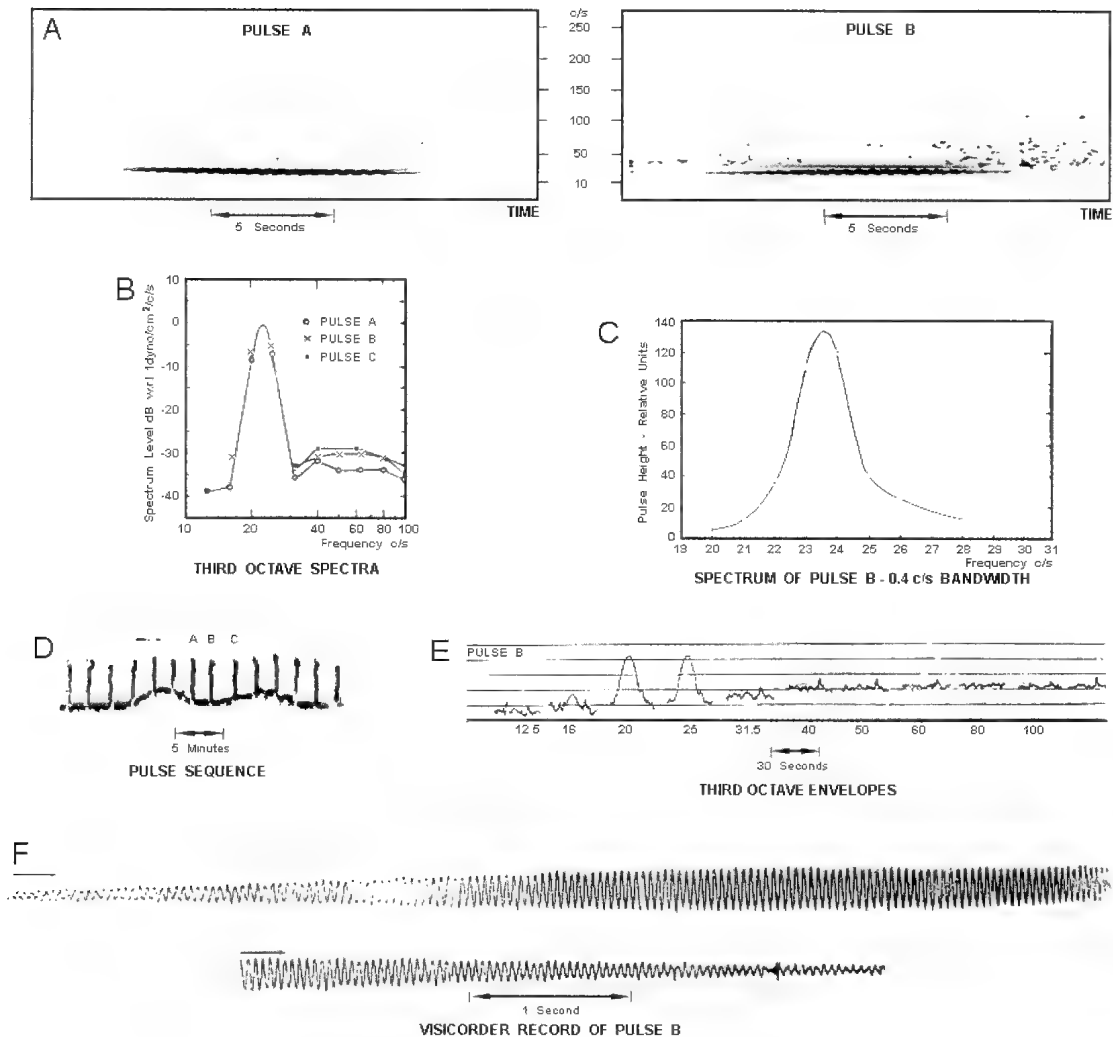


FIG. 5. '20-second' pulse. A, sonograms of two pulses. B, C, 1/3 octave spectra. D, pulse sequences. E, 1/3 octave envelopes, pulse B. F, visicorder record, pulse B.

occurring in all directions. The southern spectrum was recorded in coastal water. The influence of whales and shipping in the North Pacific is clear in the spectral difference.

**EVENING CHORUS.** The 'Barnyard Chorus' was not the only component of the sea noise to dispel the concept that the sea was an essentially quiet environment. Experience quickly revealed that a significant increase in noise level occurred twice each day. The larger increase occurred just around sunset and became known as the 'Evening Chorus', the smaller increase just before sunrise as the 'Morning Chorus'. The spectral peak in each case was around 1.2 kHz (Fig. 7).

Measurements at numerous sites in the region confirmed a similar diurnal activity and showed it was influenced by the level of solar intensity, both daily and seasonal. Investigations revealed that the common sea egg (*Evechinus chloroticus*), which is endemic around New Zealand, was the most likely source and that the spectral peak observed was related to the acoustic response of the animal during feeding. A comprehensive review of this work, which includes a comparison with similar biological choruses observed by Cato and others in Australian waters was compiled by Denham in 1994.

**VOLCANISM.** In the early days of operation, the sea-noise spectrum off Great Barrier Island was

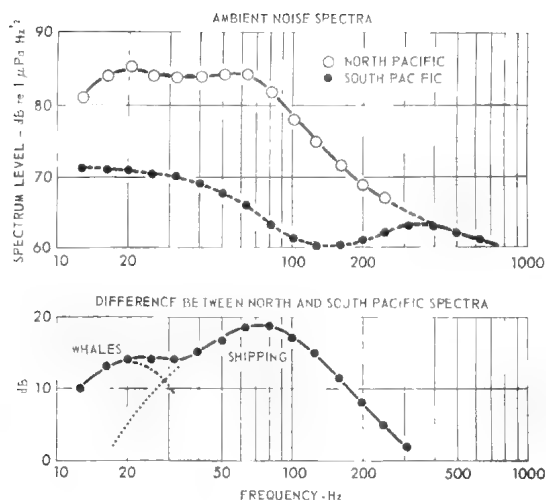


FIG. 6. Comparison of ambient noise spectra in the North and South Pacific Ocean.

at times also distorted by an intermittent low-frequency component. We came to realise that this distortion was the result of a genuine acoustic source, but in this case one of geophysical rather than biological origin, and ultimately traced it to underwater volcanism only 300km from Auckland (Kibblewhite, 1966). The active volcano lies on a line joining the active volcanic centre in the middle of the North Island with corresponding activity around Raoul Island (Fig. 3). A better picture of the level of activity became apparent when transistor technology allowed an improvement of the station's capability in 1963.

## INFLUENCE OF SEA STATE ON AMBIENT NOISE

**SEA NOISE DURING HIGH AND LOW SEA STATES.** While many sources contribute to noise in the sea, the local sea state usually provides the major input. As the spectra of Fig. 8 demonstrate, sea surface agitation and wind can significantly modify the local spectrum between 12Hz and 1200Hz. The minimum levels shown in these New Zealand spectra are low by world standards and reflect the country's isolation. While of interest in themselves, such levels posed the question as to how low the sea noise would become, if the surface-generated component could be eliminated completely. The calm waters under the ice-sheet at McMurdo Sound appeared to offer the ideal environment in which to make this assessment (Kibblewhite & Jones, 1976).

An exploratory programme was spent adopting instrumentation to withstand the rigours of the climate and in a second season of operation successful recordings were made. As a further example of the misconceptions characterising the study of this subject, we encountered an acoustic environment completely different from the one expected. The most immediately apparent feature was the high, and almost continuous, level of the biological activity. The chorus of the local seal community was the dominant feature but signals produced by cracking ice and humpback whales (perhaps up to 30km away) were also recognisable. Activity of this intensity persisted throughout the two weeks of operation and it proved difficult to identify any 'quiet'

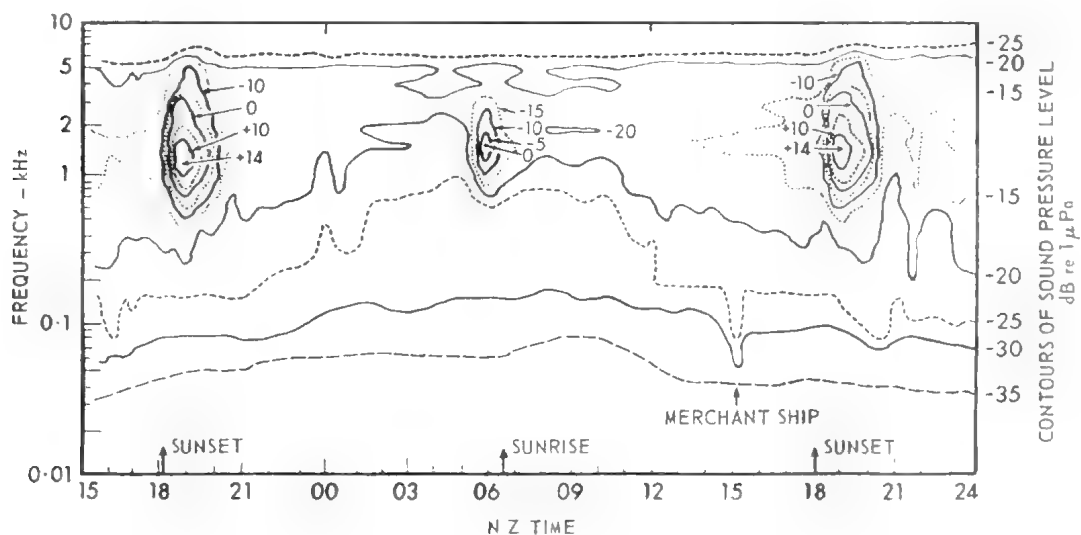


FIG. 7. Spectral contours of the ambient noise level showing the rise in activity at sunset and sunrise.

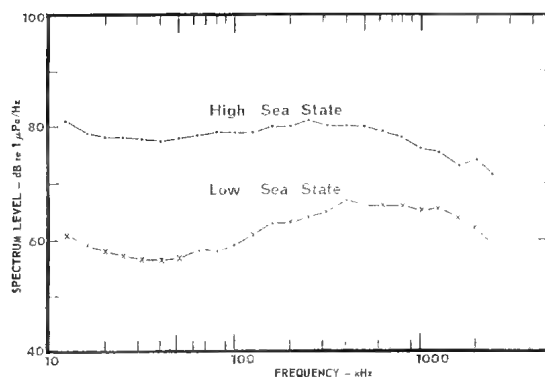


FIG. 8. Typical sea-noise spectra in high and low sea-state conditions.

periods at all. An uncontaminated sea-noise spectrum at low wind speed was however obtained. Spectral levels did indeed lie substantially below those normally associated with sea-state zero (Fig. 9).

**INFRASONIC SEA NOISE.** Our initial experience of sea-noise at frequencies below 10 Hz occurred when transistor technology first made it possible to incorporate an amplifier in the housing of the underwater hydrophone. For the first experiment a cut-off frequency of 1 Hz was selected.

Deployment of this system went very well and all were admiring its quality when a moderately severe storm blew up. To our dismay sea-noise levels rose alarmingly (in spite of the depth of deployment — approx. 250 m) and eventually overloaded the underwater electronics. Tests showed that nearly all of this unexpected noise occurred in the new band below 10 Hz. The hydrophone system was recovered and the low frequency response of the underwater amplifier adjusted, just in time to record the signal from the CHASE V explosion described earlier. The experience was again completely unexpected.

Some of the features of this infrasonic component of the sea-noise spectrum were established at the time but a full understanding had to await the technological developments which were to appear some 20 years later.

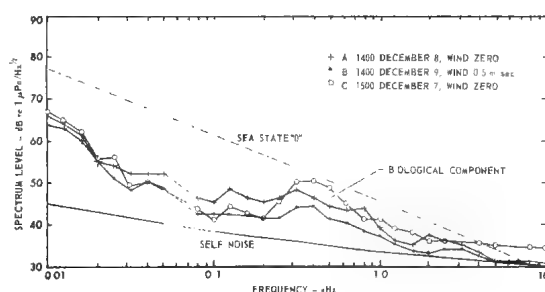


FIG. 9. Sea-state spectra at low wind speeds under the McMurdo Sound ice sheet.

Investigations by acousticians, in many parts of the world, have now shown that the high spectral levels below 10 Hz arise from a particular interaction of ocean surface-waves and are thus highly wind dependent (Kibblewhite & Ewans, 1985; Kibblewhite & Wu, 1996).

Typical sea-noise spectra between 0.1–3 kHz and wind speeds  $5\text{--}30\text{ m s}^{-1}$ , incorporating this low frequency component, are shown in Fig. 10. These infrasonic acoustic components are responsible for microseism activity which often obscures recordings of seismologists. Acousticians, however, are learning to exploit them to advantage. We have recently used them to measure the spectral properties of an offshore wave climate, using seismic sensors on land rather than the more expensive and vulnerable wave-riders at sea. It has also been shown theoretically, that certain properties of the sea-noise in this part of the spectrum are uniquely suitable for the location of oil and gas bearing

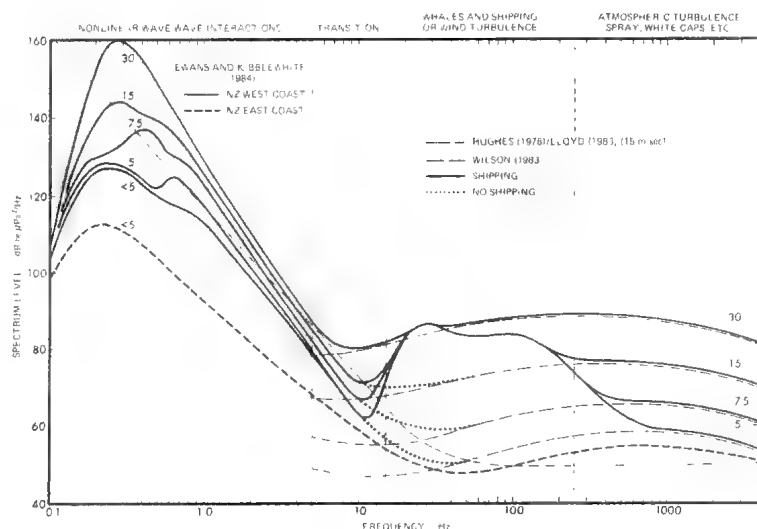


FIG. 10. Typical sea-noise spectra (0.1–3 kHz) for wind speeds  $5\text{--}30\text{ m s}^{-1}$ .



structures on the world's continental shelves. This component may therefore become critical in the search for future energy reserves (Kibblewhite & Wu, 1996).

#### DISCUSSION

It is clear that the 'Silent Sea' is anything but quiet, and instead displays the output of many contributing acoustic sources. Some of these result from environmental factors; others from biological and geophysical activity, while others are man-made. Perhaps the most intriguing, however, are those produced by cetaceans. These signals are of particular interest given that some display characteristics of language (Noad et al., 2000), the development of which has been one of the major achievements of the human race. The sounds that we recorded in the 1950s and early 1960s are now an important feature of modern research following the recognition of Northern Hemisphere humpback whale song in the early 1970s (Payne & McVay, 1971) and again in New Zealand waters by Helweg et al. (1998).

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## REVIEW OF AN ACOUSTIC ALARM STRATEGY TO MINIMISE BYCATCH OF HUMPBAC WHALES IN QUEENSLAND COASTAL GILL NET FISHERIES

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McPherson, G.R., Lien, J., Gribble, N.A. & Lane, B. 2001 12 31: Review of an acoustic alarm strategy to minimise bycatch of humpback whales in Queensland coastal gill net fisheries. *Memoirs of the Queensland Museum* 47(2): 499-506. Brisbane. ISSN 0079-8835.

Humpback whales, *Megaptera novaeangliae*, in Queensland coastal waters are at risk of entanglement in a range of fishing gears and obstacles. Since 1991 the Queensland Shark Control Programme of the Queensland Department of Primary Industries has developed an acoustic alarm bycatch reduction strategy. Four acoustic alarm types attached to gillnets have been utilised in an attempt to 'warn' humpback whales of the presence of these man-made obstacles. Another alarm type, under development, has been distributed to commercial fisheries operating in Queensland waters to reduce the risk of humpback whale entanglement in commercial gear. A standard acoustic warning protocol is under development for humpback whales, integrating specific alarm source levels, acoustic propagation and ambient noise levels. How relevant to humpback whales this standard will be is not clear, however it should provide a benchmark against which whale entanglement, or lack of it, may be compared. □ *Humpback whale, entanglement, bycatch, acoustic alarms.*

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The Queensland Shark Control Programme (QSCP) of the Queensland Department of Primary Industries (DPI) was initiated because of a series of fatal shark attacks off the Gold Coast, Sunshine Coast and other Queensland beaches in the summers of 1958-1961 (Fig. 1). The QSCP does not provide an impenetrable barrier to sharks, rather a constant fishing pressure with a combination of gillnets and baited lines that operate to reduce shark numbers in the immediate vicinity of major swimming beaches. The 'mixed gear' strategy of nets and drumlines adapts the type of gear to the physical characteristics of the swimming beach and allows for differences in catch selectivity of large individuals from a wide range of shark species. The policy has provided swimmer protection, with the incidental capture of non-target species lower than that resulting from deployment of nets alone (Dudley, 1998; Gribble et al., 1998).

Humpback whales, *Megaptera novaeangliae*, of the eastern Australian population pass southeast Queensland during their northward migration to calving areas north of Fraser Island from June-August each year. Some whales move close to Gold and Sunshine Coast beaches, often between the shark nets and the surf zone (Lien et al., 1998). After the breeding season, whales with calves move southwards to summer feeding

grounds in the Antarctic, passing southeast Queensland in September-November, again with some whales moving close to shore. QSCP records show eight humpback whales were trapped in nets between 1962-1995 off the Gold and Sunshine Coasts, with five being released and three dead in Gold Coast nets Gribble et al. (1998). No records were kept of humpback whale collisions that did not result in entrapment (Lien et al., 1998).

Lien et al. (1990) used mechanical 'low frequency clangers' (50-1000Hz), mechanical 'low frequency beepers' (3,500Hz) and electronic 'high frequency pingers' (27-50kHz) to reduce bycatch of humpback whales in Newfoundland's cod traps. The low frequency 'clangers' did not significantly reduce the probability of entrapment of humpback whales possibly due to logistic reasons. The 'low frequency beepers' did reduce the probability, while the 'high frequency pingers' did not. Due to the manner in which whales were entrapped when 'high frequency pingers' were used, Lien et al. (1990) believed that these entrapment's occurred as the whales were manoeuvring to avoid a collision. Their suggestion was that the whales detected them too late, either as they were too quiet or were detected at an insensitive part of the whales hearing spectrum.

Lien et al. (1990) concluded that humpback whales were not orienting using visual cues during inshore feeding activities in Newfoundland waters, and it was more likely that acoustical cues were the primary stimuli. The observations that humpback whales could move around and mostly avoid nets at night in extremely low light levels and in turbid water, without producing sounds, suggested that acoustic cues from the net were used.

During late 1991 Lien provided acoustic alarms of a mechanical 'low frequency beeper' type to the QSCP and supervised positioning them on the Gold Coast nets. These alarms were deployed during a 16 week period of the 1992 humpback whale migration season. No whales were caught in nets fitted with the alarms.

A paired comparison study of alternating alarmed and non-alarmed nets was commenced for a 26-week period during the 1993 humpback whale migration season. C-CORE alarms were utilised featuring a broadband signal centred on 4kHz. Towards the end of the experimental period a whale was entrapped in a non-alarmed net. The subsequent public pressure resulted in all Gold Coast nets being fitted with alarms for the remainder of the whale migration season, the change effectively terminating the experimental opportunity to examine the effectiveness of alarms.

Lien et al. (1992) demonstrated that acoustic alarms were successful in reducing humpback whale collisions with cod traps. Given that no dramatic decrease in shark catch occurred during the 1992 and 1993 acoustic experiment periods and that no whales had become entangled in alarmed nets, alarms have been routinely fitted to Gold Coast nets during subsequent whale migration periods.

In 1994 a deliberate interaction was observed between a large humpback whale and an alarmed net off the Gold Coast, with the whale circling for some time before charging the net. Smaller whales including calves had moved away as the large whale approached the net. The material, and particularly the net headropes, stretched out of the water and disintegrated under the force. While this behaviour has not been observed again, there have been three further reports of massive holes appearing in net panels and headropes of other alarmed nets on the Gold Coast and Sunshine Coast.

From 1992-1995 a single live release of a humpback whale from a non-alarmed net (due to short term logistical reasons) was recorded in a

database operated by rapid response marine rescue groups (Gribble et al., 1998). Such operations are not included in the QSCP database.

QSCP nets are not the only potential hazard for migrating humpback whales. A gillnet that appeared to be from the Australian southern shark fishery was observed entangled around a northward migrating whale off Sydney in 2000. Entanglements in anchor ropes have been reported by crews of small vessels and spanner crab pot lines have also been observed trailing from humpback whales.

A small offshore shark gillnet fishery operates within Queensland continental shelf waters, often in areas where adult whales and calves have been observed but no entanglements have been reported.

#### CRITICISM OF THE ACOUSTIC BYCATCH REDUCTION POLICY

The acoustic alarm policy developed by DPI, particularly by QSCP, has been criticised from three major viewpoints.

1) Environmental groups disagreed with the potential environmental effects of the QSCP, and considered that acoustic alarms were superfluous to a shark control operation that should not be in operation. Whatever the final biological results of analyses of the QSCP data, the outcomes will be considered primarily in the light of risk to human life and with regard to Government 'duty-of-care' legal responsibilities (McPherson et al., 1998). However, bycatch minimisation is an integral part of the QSCP strategy (Gribble et al., 1998).

2) The effectiveness of alarms, specifically the acoustic propagation of the alarms in relation to various ambient conditions, is uncertain. There was also concern that the alarms could affect the localised migratory behaviour of humpback whales, namely that alarmed nets offshore from specific headlands may direct close inshore migrating whales toward waters with unfavourable navigation conditions and higher ambient noise levels which may mask the acoustic alarm signals. While most humpback whales appear to ignore alarm signals, some approach the sound source while others withdraw from it (Todd et al., 1992). These concerns were well-founded and DPI expended research effort to assess the acoustic propagation of alarm signals in the main areas where QSCP gear was deployed. These assessments are being extended to other offshore

habitats where gear that poses a potential risk for humpback whale entanglement is deployed.

3) QSCP studies did not demonstrate sufficient statistical rigour to provide clear cut conclusions to assess the effectiveness of alarms. These criticisms were based on a premise that if something could not be demonstrated to be effective with >95% probability then there was no effectiveness and no conclusions should be drawn. The Acoustics Deterrents Workshop hosted by the U.S. National Marine Fisheries Service (Reeves et al., 1996) recognised that rigorous experimental procedures should be incorporated into any fishery study using acoustic alarms. However, the report recognised that some fisheries would never have sufficient fishing power to demonstrate statistically whether acoustic alarms could reduce marine mammal bycatch. Reeves et al. (1996) indicated that experiments that could not provide statistical probabilities beyond the most rigorous standards were still relevant provided the observations were taken in context of other observations that demonstrated the same trend. The report suggested that behavioural studies monitoring responses of mammals to dummy or 'pseudo' nets with active and non-active alarms (Koschinski & Culik, 1996; Stone et al., 1997) could provide larger sample sizes to determine effectiveness of alarms.

#### CHANGES IN RISK TO WHALE ENTANGLEMENT SINCE 1991

In 1991 the only gear that appeared to pose a threat to humpback whales in Queensland waters were eleven 186m gillnets anchored off the surf zone on Gold Coast beaches. Since that time Paterson et al. (1994) have reported increases in whale numbers of 11.7% per annum. The observations of Paterson et al. (1994) were conducted off Stradbroke Island immediately north of the Gold Coast. It is not clear what proportion of the humpback whale population observed from Stradbroke Island passed within close proximity of Gold Coast QSCP nets, although it is reasonable to assume that the number passing the Gold Coast has increased in proportion to the population increase.

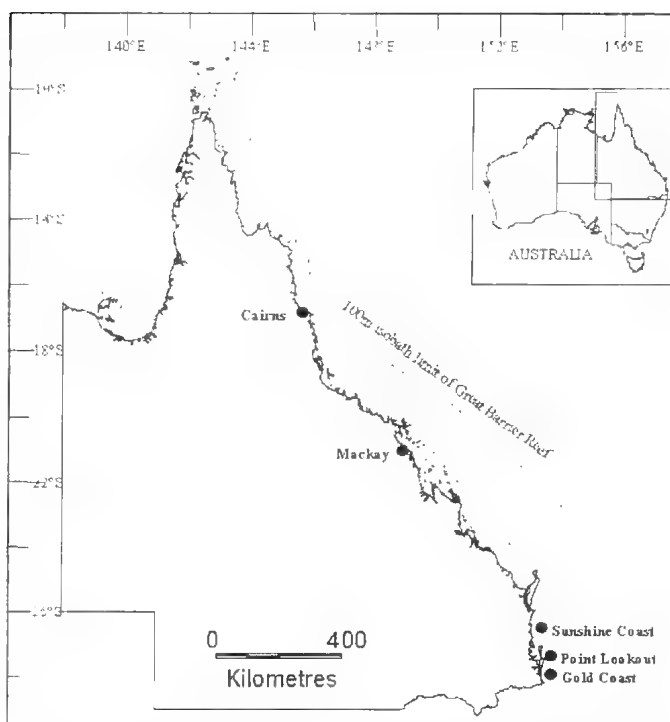


FIG. 1. Map of Queensland showing selected Queensland Shark Control Programme contract locations.

With the steady increase in numbers humpback whales have appeared in waters where they had not been observed, at least over the past 35-40 years. There is anecdotal information from QSCP contractors (e.g. J. Backmann, pers. comm.) indicating that humpback whales had previously visited those areas, but not since the mid 1960's, prior to when the eastern Australian population was reported to have been at its lowest (Paterson et al., 1994). In 1996 a humpback whale calf was entangled in a QSCP gillnet off the Sunshine Coast (NW of the Gold Coast) during the southward migration and, as a result, was temporarily beached in the surf zone. In 1997 near entanglements occurred off the harbour mouth at Mackay (Fig. 1). Acoustic alarms have now been attached to QSCP gillnets at Mackay (5) and Sunshine Coast (11).

#### FIELD AND ANALYTICAL METHODS

Acoustic signals from alarms were recorded with a GEC-Marconi SH101X calibrated 100kHz hydrophone, a low noise Royal Australian Navy Research Laboratory pre-amplifier and a Sony TCD-D8 DAT recorder. The system had a frequency response of 15-22,000Hz. Tapes were

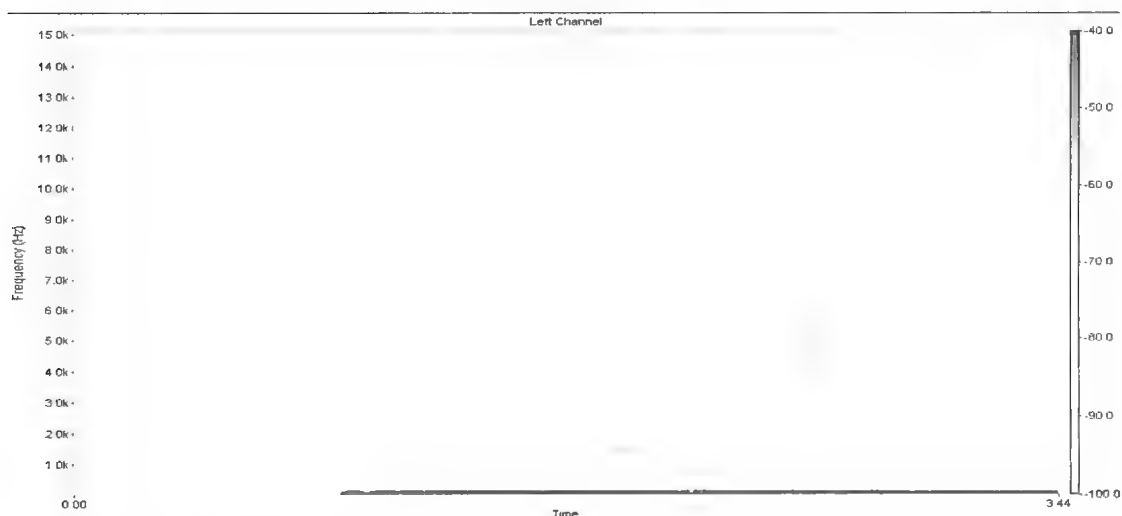


FIG. 2. Spectrogram of repeated signals from at least six C-CORE mechanical alarms (vertical broadband signals between 2-12kHz), three Dukane 'Netmark' alarms (horizontal tone burst at around 11 kHz) and humpback song components off the Gold Coast. C-CORE and Dukane alarms were on a net 100m from the hydrophone, and possibly another further away. Location of the calling whale was not known.

analysed using 'Spectra Plus' acoustics software with an AWE-64 sound card at a sampling rate of 44,100Hz, with a Fast Fourier Transform (FFT) of 1,024 points and a filter bandwidth (FFT bin width) of 43.07Hz. When measuring the levels of the fundamental frequencies of the alarms, no correction was made for the filter bandwidth because of the sinusoidal character of the signals. Sound pressure levels (SPL) were expressed as dB re  $1\mu\text{Pa}$ . The analysis system was calibrated with a Tektronix TDS-210 digital oscilloscope with an FFT spectrum analyser module.

Background noise spectrum levels (in 1Hz bands) were calculated from the FFT results by correcting for the filter bandwidth from the level in the FFT bin (values given are in dB re  $1\mu\text{Pa}^2/\text{Hz}$ ). One-third octave bandwidth levels were estimated by adding the bandwidth correction for the 2,810-3,540Hz 1/3 octave band to the spectrum level.

#### ACOUSTIC ALARM VARIATIONS

Since 1991 four acoustic alarms types have been used to 'warn' humpback whales of the presence of QSCP gillnets. Original alarm deployments were courtesy of Jon Lien who provided mechanical type alarms centred around a fundamental frequency of 4.0kHz that had been used effectively to enhance the acoustic signature of cod traps (Lien et al., 1992). Source levels were up to 145dB re  $1\mu\text{Pa}$  at 1metre. These had shown

to draw the attention of whales to the sound source, which upon closer inspection was avoided along with the gillnet to which it was attached.

Corrosion and damage incurred by net hauling operations rapidly reduced the number of working alarms. These were replaced during the 1994-1996 migrations by 'C-CORE' alarms (Centre for Cold Ocean Research Engineering, Memorial University of Newfoundland, Canada). The acoustic signature of these mechanical alarms featured a broadband range from 2~12kHz. A spectrogram of C-CORE alarms and 'Dukane' high frequency alarms (Dukane Corporation, Seacom Division, IL, USA) is given in Fig. 2. As some acoustic energy occurred <2.0kHz, which approaches the known audible capacity of most shark species investigated (Corwin, 1981), there was concern that sharks, the target species of the gear, would detect the acoustic signal. Given the short duration that the alarms were deployed on QSCP gillnets, no consistent trend in shark catch was detected. Concerns were also expressed that the electromagnetic nature of the C-CORE alarm signal may affect catches although no data are available on this aspect of performance.

On Lien's second visit to Queensland he supervised the development of a piezo buzzer type alarm, similar to his earlier design and described by Lien et al. (1995). At that time the 50mm diameter plastic sewer pipe and

appropriate end caps and threaded fittings used in Canada and USA were not available in Cairns, Australia. The nearest equivalent pipe was 100mm diameter. To minimise damage due to water intrusion, the piezo buzzer (a truck reversing alarm with a fundamental frequency centred around 2.9-3.0kHz) was set in resin in the base of the unit with only the terminals exposed. Acoustic output of the alarms were not as high (source levels ~125-130dB re 1 $\mu$ Pa at 1m) as the original alarm described by Lien et al. (1995). The new alarm was ~3 times heavier due to the volume of materials used and trials indicated that alarm source levels declined as alarm weight increased. In many alarms the sound pressure level of the second harmonic frequency was higher than the fundamental frequency. Nonetheless, this inexpensive alarm (~AUD\$20), was utilised during the 1997-1998 humpback whale migration seasons with no entanglements on alarmed nets resulting.

Overall size of these 100mm diameter alarms introduced a range of logistical problems associated with deployment on gillnets which resulted in a substantial loss rate from the gear. The QSCP called for expressions of interest for the construction of a replacement alarm and a tender for supply was let to BASA Technical Services (BASA Technical Services, Brisbane, Australia). BASA produced a piezo buzzer alarm with a fundamental output at ~3.4kHz. The alarm was relatively small and used four 1.5V batteries which proved to be light and cost effective. The spectrum is given in Fig. 3; source level exceeded 140dB re 1 $\mu$ Pa at 1m. Longevity of the signal has yet to be determined although it is anticipated to be ~21 days continuous operation.

McPherson et al. (1999) described the acoustic features and construction of the Lien (Cairns) piezo alarm, a development of the original piezo alarm described by Lien et al. (1995). Further work has increased the longevity of these alarms to 40 days continuous operation and the alarm is seen as a cheaper variation suitable for deployment within Queensland commercial fisheries, at least until a full production commercial model is available. Environment Australia has funded DPI to continue development and construction of this alarm type for immediate use within commercial fisheries that may take marine mammals. One hundred alarms have been constructed with a number having been provided to gillnet operators to conduct logistical gear deployment trials including attachment to nets, operating depth and vessel storage.

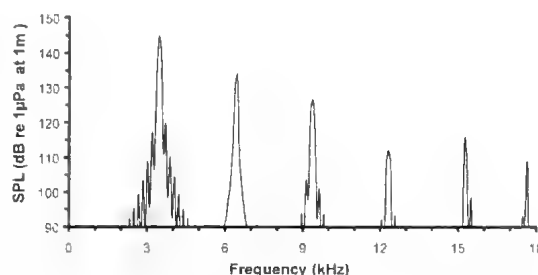


FIG. 3. Spectrum of BASA Technical Services 'whale' alarm.

#### CURRENT STATUS OF ACOUSTIC ALARM STRATEGY

Research is continuing on the acoustic propagation of alarm signals of the lower frequency alarms (~3kHz fundamental frequency, considered to be most effective for humpback whales) within different environments. QSCP areas include close proximity to high wave energy sand beaches in 5-10m water off the Gold and Sunshine Coasts, and both deeper and shallower waters with more mud bottoms in northern waters. Commercial fishery areas include shallow nearshore environments to more offshore waters between the coast and Queensland's coral reefs in 20-30m.

Alarm performance attributes such as source levels, total acoustic intensity of short tone bursts relative to ambient sound levels, and alarm longevity are being developed and assessed. Until the BASA and Lien (Cairns) alarms currently in use have attained their full development potential, specific recommendations on alarm deployment on obstacles in Queensland waters cannot be made.

The threshold for auditory detection of a signal is considered to occur when the signal level equals the background noise level in a certain bandwidth, known as the masking band (Richardson et al., 1995). Noise outside this band would have little effect on the detection of signals. Research on hearing in marine mammals has shown that a range of values for the width of the masking band exists for tonal signals. Most results vary between 1/6 and 1/3 of an octave, although some are less (Richardson et al., 1995); the most conservative approach is to assume a masking band of 1/3 octave. As the fundamental frequency of the present BASA whale alarms and Lien (Cairns) alarms fall within the 1/3 octave band of 2,810-3,540Hz, the signal-noise-ratio

(SNR) of alarm tone bursts are compared to the background noise within this 1/3 octave band.

Background ambient noise levels include biological noise such as snapping shrimp, wave motion and breaking surf within 20-80m from the nets, depending on tide state. Considerable variability has been detected between different beaches within QSCP contract areas. Ambient levels may change with sea state and wind strength, while at more sheltered beaches ambient noise may be dominated by snapping shrimp with spectral levels between 65-80dB re  $1\mu\text{Pa}^2/\text{Hz}$  at 3kHz irrespective of weather conditions. Ambient levels in fishing areas inside the Great Barrier Reef where water depth is >20m appear to be dominated by fish choruses that may reach spectral levels of 65dB re  $1\mu\text{Pa}^2/\text{Hz}$  at ~3kHz (R. McCauley, pers. comm.).

There are few biological data to determine the most appropriate positioning of alarms on nets in relation to auditory capacity of marine mammals and background noise. Kraus et al. (1995) spaced 10kHz alarms at distances where SPL's had dropped to a SNR of +15dB and demonstrated a significant reduction in bycatch of harbour porpoise. Gearin et al. (1999) placed alarms a distance apart that permitted harbour porpoise to hear 3kHz alarms at a SNR of +10dB up to a Beaufort sea state of 4 (i.e. 11-16 knots).

As spacing between alarms increases it heightens the chance of an acoustic 'hole' occurring for an animal approaching a point on the net, or gear, midway between two alarms. The only discernible acoustic cues would be on either side of the approaching animal, but not directly ahead. Acoustic 'holes' would be more significant where the range from the line of sources is less than the source spacing, which would normally be the case of interest. In this situation, the received signal would be dominated by the contributions of the closest two alarms, and the contributions from other alarms could be neglected. The received signal is lowest when the receiver (animal) is on a line which crosses the line of alarms at right angles and mid-way between two adjacent alarms.

The minimum distance from the net that provides humpback whales sufficient time or space to avoid a collision was considered to be 15m based on the maximum length for the species. Lien et al. (1990) and Lien et al. (1992) indicated that the circumstances in which humpback whales were caught in both alarmed and non-alarmed nets suggested that in some

instances the whales were attempting to avoid the gear, but probably detected it too late to avoid collision. No SNR data were available for these experiments.

For a particular background noise level, the spacing of alarms required to give a minimum SNR of a chosen value of +10dB (or the more conservative +15dB) within 15m of the net can be determined using the method given by McPherson et al. (1999). Assessment of alarm signal propagation and ambient noise levels is conducted for each beach within QSCP contract areas, or commercial fishery areas. Under most alarm, propagation and ambient level conditions, a +15dB SNR is achieved 15m out from each net between adjacent alarms, if alarms are spaced 50m along the net. As QSCP nets are 186m in length, contractors are currently required to position five alarms on gillnets a minimum of 45m apart, to achieve this SNR/distance out scenario.

Whether the +15dB SNR at 15m from the net scenario is appropriate is not known, however it is a minimum or known acoustic standard against which whale entrapments, or lack of them, can be compared.

## FUTURE RESEARCH

Environment Australia has funded DPI, University of Queensland, Memorial University of Newfoundland, SEANET and Queensland Parks and Wildlife Service to examine the behavioural responses of dugongs and dolphins to acoustic alarms. Funding has also been provided for the further development of the Lien (Cairns) alarm for deployment throughout Queensland's gillnet fisheries, including those that may interact with humpback whales. It is hoped through these experiments we will come to more fully assess bycatch in gillnet fisheries and develop effective means to minimise it.

DPI does not believe it would be appropriate to conduct acoustic alarm research that may jeopardise the lives of marine mammals simply in order to achieve more rigorous experiments that would demonstrate >95% probability of effectiveness for alarms. Gribble et al. (1998) described the level of bycatch of marine mammals in Queensland gillnet fisheries as probably minor and there will be no attempt to raise fishing effort to increase bycatch numbers simply to achieve a statistical probability.



## ACKNOWLEDGEMENTS

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# A COMBINED ACOUSTIC AND VISUAL SURVEY OF HUMPBACK WHALES OFF SOUTHEAST QUEENSLAND

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During their migrations between low latitude breeding areas and high latitude feeding areas, male humpback whales, *Megaptera novaeangliae*, are frequently heard singing, often continuously for many hours, and the sounds are audible for tens of kilometres. The stock that passes close to the coast of southeast Queensland has been extensively surveyed visually, but little is known of movements of whales that pass out of sight of land here, or in other areas of the world, where the migratory paths of humpback whales are often across open ocean. Acoustic surveying may be useful in quantifying whale movements in oceanic waters beyond the range of land surveying and an addition to visual monitoring. For acoustic surveys to be of use, the acoustic cues of the whales must be quantified and calibrated against the numbers of whales in an area. In 1997 we performed a combined visual and acoustic survey of whales migrating close to shore on the coast of southeast Queensland. Song activity was measured using two indices: number of passing singers and number of singer-hours observed within a 10km sector, and correlated with the number of whales passing through the area determined visually. Both were significantly correlated with  $r = 0.68$  and  $0.64$  for singers and singer-hours respectively on a daily basis, and  $0.79$  and  $0.89$  respectively on a weekly basis. Linear regressions of daily measures of song activity with numbers of whales seen lead to estimates of ratios of singers with whales seen of  $0.127 \pm 0.027$  (95% confidence interval) and singer-hours with whales seen of  $0.288 \pm 0.065$ . We discuss the possible use of these indices for conducting stand-alone acoustic surveys.  $\square$  *Humpback whale, acoustic, song, migration, Australia.*

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Traditionally, surveys of whales have been conducted using visual detection from elevated points along coastlines or from ships or aircraft. Visual surveys are limited primarily by the cryptic nature of cetaceans which spend much of their time underwater and are available for sampling only for the short proportion of time spent at the surface. They are also limited in their range of detection (particularly for ship-based surveys), are highly weather dependent and are restricted to daylight hours.

Many species of whales produce intense sounds that are audible to substantial distances and thus may be useful in surveying, especially in conditions where visual methods have limited effectiveness. Acoustic surveys have potential advantages over visual surveys: large cetaceans in particular may be detectable at many times the range possible with visual observations; detection is less dependent on weather; no restriction to daylight hours; and can be automated to varying extents (e.g. Thomas et al., 1986; Cummings & Holliday, 1985; Clark et al., 1986; Gillespie, 1997; Clark &

Frstrup, 1997; Norris et al., 1999). While visual observations are limited to the small proportion of time that whales are at the surface in the field of vision, acoustic detection can be omnidirectional and possible for as long as the whales are vocalising. Deployment of automated acoustic recording systems that record for long periods (to be analysed after recovery) may be less expensive than ship-board surveys since they would require less ship time, and especially if analysis was automated. They are also non-intrusive and minimise sampling bias.

Acoustic surveying also has its limitations, the greatest being that it is indirect, i.e. counting cues rather than whales, and so requires careful calibration of the relationship between the occurrence of sounds and the numbers of whales (Buckland et al., 1993). It is effective only for species that vocalise regularly and, of those, only a portion of individuals in a stock may vocalise at any time. Also variations in background noise levels and local sound propagation characteristics

cause significant variation in the distances of detection of vocalising whales.

Determining the spatial concentration of sources from the sounds detected, necessary in any estimate of abundance, is difficult without fixing the source positions. This usually requires three or more well spaced receivers with accurately known positions (e.g. Watkins & Schevill, 1972; Cummings & Holliday, 1985). This significantly increases cost, complexity of the work at sea and the amount of analysis required. Under certain circumstances, simpler methods are effective in determining the distances of the sources which can be related to source concentration (Cato, 1998).

Despite the potential of acoustics, few attempts have been made to calibrate acoustic cues against visual counts, particularly for mysticetes. The most extensive acoustic-visual surveys have been of bowhead whales (*Balaena mysticetus*) during their annual migration off Point Barrow, Alaska (Cummings & Holliday, 1985; Clark et al., 1986, 1996; Clark & Ellison, 1989, 2000; Rafiery et al., 1990; Würsig & Clark, 1993; Zeh et al., 1993; Rafiery & Zeh, 1998). Difficult weather conditions and the use of ice as a survey platform often severely restricted visual surveys of these whales. Arrays of fixed hydrophones have been used to track vocalising bowheads concurrently with visual observations, and mark-recapture and other statistical techniques have been applied to both data sets in an attempt to obtain more accurate population estimates (Gentleman & Zeh, 1987; Rafiery et al., 1990; Zeh et al., 1993). Clark & Fristrup (1997) used a different approach to compare and calibrate acoustic and visual detection rates for blue whales (*Balaenoptera musculus*) and fin whales (*B. physalus*) during ship-based line transect visual and acoustic surveys combined with static hydrophone arrays. A statistical combination of acoustic and visual data attempted to improve density estimates (Fristrup & Clark, 1997). McDonald & Fox (1999) used an acoustic-only approach with a single bottom-mounted hydrophone to estimate minimum densities of fin whales off Hawaii.

Common to all these acoustic surveys has been the use of acoustics either to gather additional information to support limited visual surveys where the probability of visual detection is low or has not been previously determined, or as an almost entirely uncalibrated survey tool.

Humpback whales offer an opportunity to develop acoustic monitoring techniques using populations that can be well surveyed visually. Like many species of baleen whales, they undertake annual migrations from high latitude feeding areas to low latitude breeding areas. Humpback whales are often distributed along coastlines during part of this annual cycle, particularly on their breeding grounds which tend to be in shallow tropical waters (Dawbin, 1966) making them relatively accessible for surveying.

Many techniques have been used for visual surveys of these whales including aerial surveys (Herman & Antinofa, 1977; Bryden, 1985; Bannister, 1985; Bannister et al., 1991; Corkeron et al., 1994), ship-based surveys (Chittleborough, 1965; Herman & Antinofa, 1977; Whitehead, 1982; Stone & Hamner, 1988; Mattila & Clapham, 1989; Mattila et al., 1994), mark-recapture surveys using photographic identification of individuals (Whitehead, 1982; Baker et al., 1985; Darling & Morowitz, 1986; Baker & Herman, 1987; Flórez-González, 1991; Darling & Mori, 1993; Smith et al., 1999), and direct land-based counts of whales along migratory corridors (Bryden, 1985; Paterson & Paterson, 1989; Bryden et al., 1990, 1996; Paterson et al., 1994, 2001; Findlay & Best, 1996b). These surveys have been used to estimate absolute population levels, relative abundance and population growth rates, or population densities for specific areas.

Humpback whale vocalisations are also comparatively well studied. Male humpback whales produce long, complex vocalisations on the breeding grounds and during migration (Kibblewhite et al., 1967; Payne & McVay, 1971; Winn & Winn, 1978; Cato, 1984, 1991). These songs may be produced continuously for many hours at relatively high source levels. The combination of coastal distribution and reliable and distinctive vocalisation make humpback whales an ideal model for the development of acoustic surveying techniques.

Previous acoustic surveys of humpback whales have been conducted. Winn et al. (1975) performed ship-based visual and acoustic surveys on humpback whales in the West Indies to determine a population total for the breeding area, while Levenson & Leapey (1978) used a different technique to survey the West Indies, dropping sonobuoys from the air. Both studies made assumptions concerning the maximum detectable range of singing humpback whales

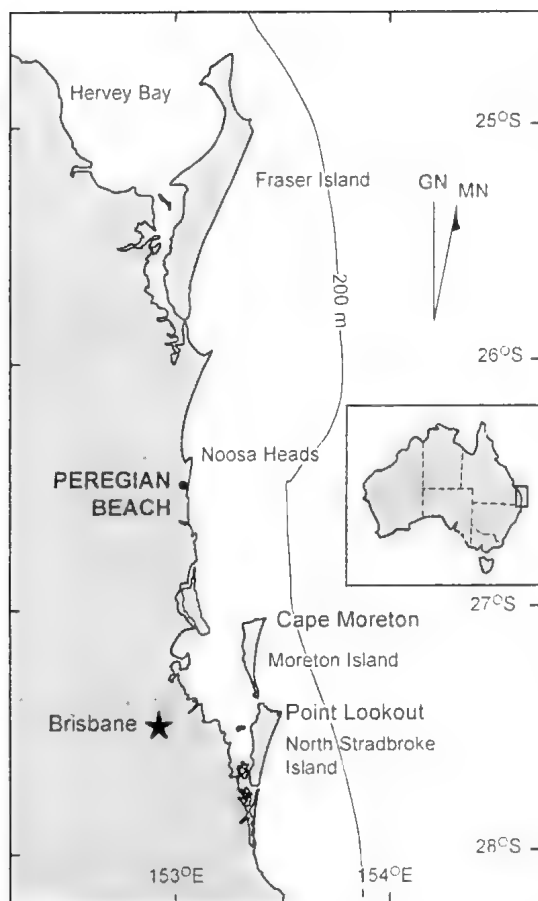


FIG. 1. Southeast Queensland showing study site of Peregian Beach and its westward location from other study sites of Point Lookout and Cape Moreton.

(12.8 and 9.3 km respectively) without apparently determining local propagation characteristics and with only limited data available concerning source levels of song. Although Winn et al. attempted to develop a ratio of 'callers' to 'non-callers' based on 11 visual sightings, ratios varied widely for different areas leading to the conclusion that this ratio 'represents the greatest weakness in the acoustic method'.

Several subsequent acoustic surveys of humpback whales have simply relied upon the presence or absence of song to determine the migratory paths or distribution of whales (Clapham & Mattila, 1990; Dawbin & Gill, 1991; Gill et al., 1995; Norris et al., 1999). Frankel et al. (1995) used an array of hydrophones to determine the density of singers off Hawaii but did not attempt to relate it to the numbers of

whales seen. Au et al. (2000) used remote recording techniques to show variations in singing activity across the winter and diurnally in Hawaii, but did not attempt to relate measurements of acoustic activity with singer density or abundance. They did, however, suggest that such stand-alone acoustic techniques could be used to provide either relative abundance estimates of humpback whales, or, if ground-truthed with visual and acoustic-positional surveys, absolute abundance estimates.

Land-based visual surveys along the migratory corridor on the east coast of Australia have been conducted regularly since 1978, mainly from Point Lookout on North Stradbroke Island with some from nearby Cape Moreton on Moreton Island (Fig. 1), by two independent survey groups (Paterson, 1984; Paterson & Paterson, 1984, 1989; Paterson et al., 1994, 2001; and Bryden, 1985; Bryden & Slade, 1988; Bryden et al., 1990, 1996). Despite some differences in survey design and statistical methodologies, the two surveys are in broad agreement regarding both absolute and relative abundance, for example, Paterson et al. (1994) and Bryden et al. (1996) reporting populations of 1900 for 1992 and 1807 for 1993 respectively, with annual population growth rate estimates of 11.7% and 12.3% respectively. Humpback whales have also been shown to sing reliably in this area during migration (Cato, 1984, 1991; Noad et al., 2000; Macknight et al., 2001).

In this study, visual and acoustic surveys were performed simultaneously on this well described and surveyed migratory population of humpback whales off southeast Queensland to examine the possible use of acoustic stand-alone surveys for surveying humpback whale populations. Correlations between the number of whales visible and those singing are determined, and ratios of whales to measurable indices of acoustic activity are developed for future use in acoustic surveys.

## MATERIALS AND METHODS

Visual and acoustic observations were conducted at Peregian Beach (26°30'S, 153°07'E) on the southern coast of Queensland (Fig. 1). The coast here comprises a long, straight, gently shoaling, sandy beach, the nearest headland 6 km to the south. Data were collected during the southward migration of the whales in 1997, between 28 August and 31 October.

**VISUAL DATA COLLECTION.** Visual observations were made from the 73 m high peak of a nearby hill, Emu Mountain, set 700 m back

from the beach. The view was unobstructed in all directions, coastal features allowing a 145° view of the ocean to the horizon (~30km). Two teams of 3-5 volunteers made observations in four shifts from 7am to 5pm daily. Position, composition and behaviour of whale groups were recorded. A theodolite was used to measure horizontal and vertical angles to whale pods with measurements calibrated by comparison of theodolite-tracked boat positions with GPS positions determined in the boat at the same time. At ranges of up to 10km the accuracy was determined to be within the differential error of the GPS and so was taken to be within 100m.

Data were also collected regarding environmental factors that might affect visibility or sightability including wind speed and direction, sea-state, cloud cover, glare, precipitation and air clarity. The number, type and positions of ships and boats were also recorded. Observations were abandoned in conditions of poor visibility or sightability including heavy or steady rain, and sea-state >4.

Data were entered into a spreadsheet daily (Excel, Microsoft) which calculated the positions of pods using the theodolite measurements. These calculations included the measured height of the theodolite above the peak of the hill, the tide height and a refraction coefficient ( $k = 0.08$ , see Appendix). Pod identities and continuity of sightings determined by the observers were checked against measured positions for consistency.

Aerial surveys out to 60km from shore in good visibility by Bryden (1985) indicated that <5% of humpback whales passed beyond 10km of the headlands of North Stradbroke and Moreton Islands, where most visual surveys have been conducted. He considered that 10km was the useful limit of visibility from shore under good conditions. Peregrine Beach is ~100km north of Point Lookout (on Stradbroke I.) and ~45km west (Fig. 1). While we saw many whales at ranges far greater than 10km, we have limited this analysis to whales seen within 10km of shore. The closest approach of whales was only a few hundred metres offshore and so our observation area was considered to extend from shore to 10km seaward, and limited north and south between bearings 10° and 160° on the study grid (Fig. 2). The visual survey area was not centred on Emu Mt as it was inland from the coast and so would have included a significant area not available to migrating whales, and would have been less directly comparable with the acoustic survey area. Whales were seen travelling both northwards and

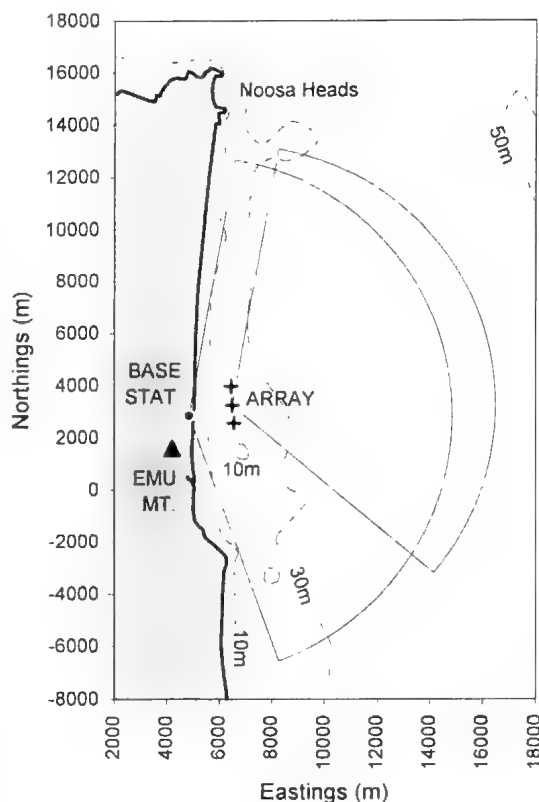


FIG. 2. Peregrine Beach study site showing observation areas and grid system used (grid north lies between true and magnetic north). Visual observations were made from 73m high Emu Mt while acoustic recordings were made using three offshore hydrophones (crosses). The small shoal south of the array caused sudden and profound attenuation of song sounds of singers in the southern portion of the study area.

southwards although some whale groups did not have enough sightings to determine direction of movement. These were assigned a direction according to the ratio of north-south whales observed during that day.

**ACOUSTIC DATA COLLECTION.** An array of three custom-designed hydrophone-buoys (A, B and C) was deployed 1,500m offshore in 20m of water (Figs 2,3). The hydrophone-buoys were spaced in a line ~750m apart, giving an array base-line of ~1,500m, with the central buoy B slightly offset to the west. Each buoy was moored by a 40kg concrete and steel clump attached to 6m of chain and a 4.5kg plough anchor. The body of each buoy was a hollow tube of PVC pipe supported by a fibreglass foam-filled 'torus' float. Each contained a sonobuoy VHF transmitter

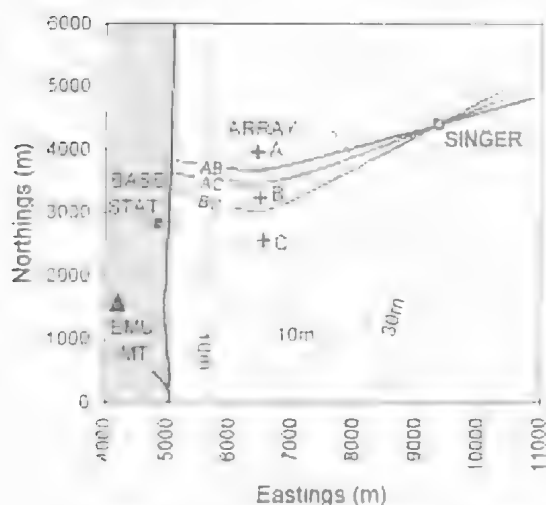


FIG. 3. Acoustic positioning of a singing humpback whale. Differences in the arrival time of sounds from the singer to each of the hydrophones were used to generate a hyperbola (grey line) for each pair of buoys. The point of intersection of the three hyperbolae (from buoy-pairs AB, BC and AC) was taken as the position of the singer. A small discrepancy in intersections resulted in a triangle, in which case the singer was taken to be at the centre.

(Spartan Electronics AN/SSQ 41B) and a rechargeable battery pack (12V, 30A-h) and were designed to follow the rise and fall of the sea surface and remain upright, thus optimising the orientation of the transmitter antenna. This was achieved by attaching the mooring line at a point in relationship to the distribution of mass that minimised rotation in the vertical plane. A 40dB gain pre-amplifier (custom-built) was contained in a separate underwater housing attached to the mooring clump and connected to the buoy by standard RG58 coaxial cable (single core, 50Ohm) running along the anchor rope. A GEC-Marconi SH101X hydrophone was connected to the preamplifier by 10m of RG58 cable and was suspended from a small float attached to the anchor, approximately 1m above the substrate. The hydrophone cable was wound with string to help prevent low frequency vortex-shedding noise in conditions of significant current or groundswell.

Signals from the buoys were received by a Yagi antenna mounted as high as possible (~10m above sea-level) at the base station located 80m behind the beach. The antenna was connected to a four channel, low noise, VHF receiver. Signals from the receiver were split and passed to two desktop computers (IBM PC clones) – one for

real-time spectrographic monitoring and the other for computation of singer positions – a four-track analog tape recorder (Tascam 424 Portastudio) and a stereo DAT recorder (Sony TCD-D7 Walkman). The audio signal was monitored continuously during the hours of visual observations. When a singer was detected with a signal-to-noise ratio sufficient to allow the pattern of the song to be determined, recording was initiated. Some tracking of singers occurred in real-time in the field while the majority occurred at a later time using the multi-track recordings.

Appropriate sounds in the song (rapidly frequency-modulating tonal sounds) were manually selected and sampled into the computer using Cool Edit 96 (Syntrillium). Matlab (Mathworks) customised software performed waveform cross-correlations of the same sound received on each of the three pairs of hydrophones (buoy-pairs AB, BC and CA) to determine the time-of-arrival-differences (TOADs) for each pair of buoys. Each of the three resulting TOADs was used to generate a hyperbola along which the source of the sound could lie. The intersection of the three hyperbolae was taken as the position of the singer (Fig. 3). While there is ambiguity inherent in this method (since the hyperbolae intersect at two points, one each side of the line of hydrophones), in our experiment the westerly solution was usually inland and could be discarded. Sequential calculation of positions allowed the singer to be tracked (Fig. 4).

*Calibration and Ranging Error.* The array was ground-truthed using two methods. The first was comparison of acoustically calculated positions with theodolite positions of visually identified singers (based on the timing of surface intervals predicted acoustically by features of the song) (Fig. 4). The second was experimental and involved the implosion of light bulbs under the research vessel at various locations in the study area. These bulbs, smashed at depth, produced a single brief popping sound audible at several kilometres range that could be acoustically positioned for comparison with GPS positions. Bulbs were enclosed in a fine net so that broken debris could be recovered.

As three hydrophones were necessary to calculate the location of the singer, acoustic tracking was not possible if one or more of the buoys was not operating. Time lost due to technical problems was minimal although the



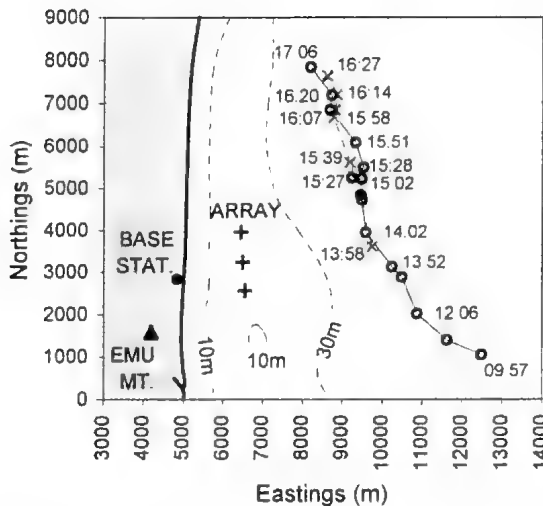


FIG. 4. An example of a combined visual and acoustic track of a singing humpback whale (70904s1) including times of locations. Acoustic positions are black circles and theodolite-generated visual positions are grey crosses.

buoys were removed from the water in the middle of the survey period for scheduled maintenance.

*Quantification of Singing Activity.* Although some singers passed very close to the array, only one singer went inside the array and then by only a few tens of metres. The area used for the acoustic survey was therefore taken as being a 10km sector out to sea from the array between the bearings  $10^\circ$  and  $130^\circ$  (Fig. 2) where the acoustic tracking was found to give reliable results. Although this did not correspond exactly to the 10km sector from the beach used for the visual survey, the two sectors overlapped substantially and could be considered to provide comparable visual and acoustic samples of the migrating whales.

Within this sector, the signal-to noise ratio (SNR) of the sounds used in the cross-correlation analysis was more than adequate for the purpose. The SNR of 'modulated bellows', the sound most frequently used, were calculated for 20 singers at 92 points within 13km of the array by measuring the relative levels of the signal and the background noise in the  $1/3$  octave band containing the centre frequency of the signal (210-400Hz), averaged over the duration of the sound (approx. 1.2sec). The mean SNR at a range of 10km was 22dB under average observational conditions.

Only song recorded during hours of visual survey were included in this analysis. As most

visual observations were curtailed due to high sea-state and rain, and similar conditions also reduced singer detectability due to increased ambient noise, this ensured that visual and acoustic observations were directly comparable under favourable detection conditions.

Two methods of quantifying singing activity were used: 'number of singers' which was a count of the number of individual singers passing through the sector per 10 hours, and 'singer-hour index' which was determined by counting the number of singers in the area each hour of the 10-h observation day and summing the results for the day.

The 'number of singers' was the acoustic analogy of the visual count of number of individuals passing through per 10h. Singing was considered to be from the same whale if the song was heard continuously with only short gaps of a few minutes between song cycles, and no significant change in source position occurred. Where the gap was longer, we assumed that it was from the same whale if the position of the new song-session was close to that of the original song-session, if the song contained idiosyncrasies of pattern consistent with the original singer, or if the singer was tracked visually between singing locations. This method provided a direct measurement of the true number of individuals singing as they passed through the sector in the 10-h observation day, but required substantial effort, since all singers had to be tracked acoustically throughout the full observation period.

The 'singer-hour index' was determined by counting the number of singers detected within the sector once per hour and summing the results for all hours of the observation day. To avoid missing a singer during the pause between song cycles, a 10min period was monitored every hour, from 5min before the hour to 5min after the hour. This method provided a relative index of singing activity related to the number of singers and the duration of singing, since an individual singer would be counted for each hour that it is audible. The purpose of measuring this index was to test its effectiveness as a relative indicator of the number of whales passing, since it was less time consuming to measure than the actual number of singers. It did not require identification of individual singers or their locations, apart from an estimate of their ranges. In this test, the range was determined using the three-hydrophone localisation method described above, but simpler

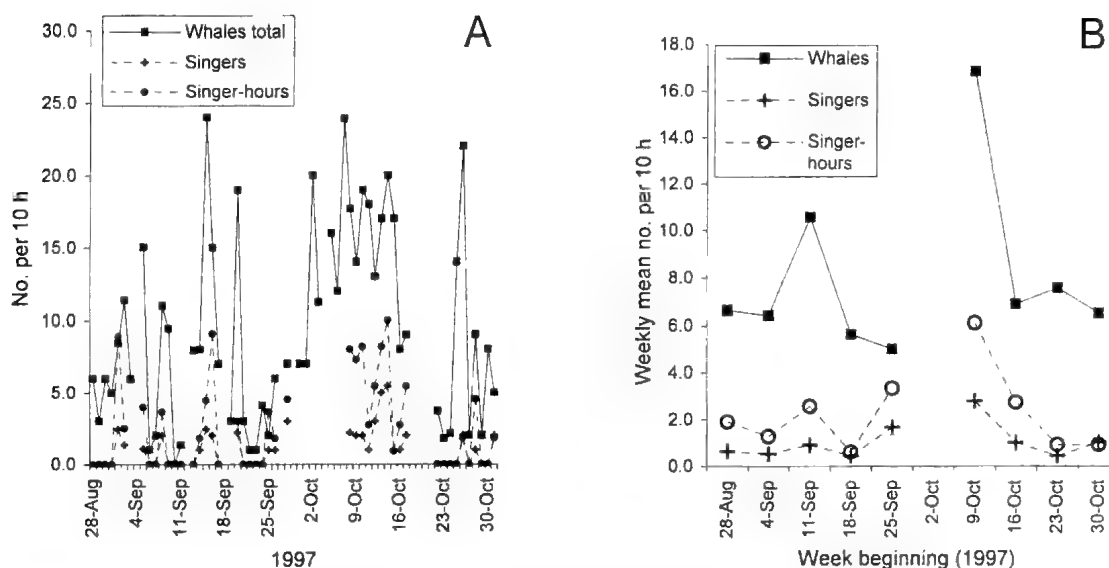


FIG. 5. Fluctuations of humpback whale visual and acoustic counts during the study period; all data averaged for 10-h sampling periods. A, daily fluctuations; B, weekly fluctuations. All visual data are shown for daily fluctuations whereas weekly averages are based only on days where both visual and acoustic data were collected. The week beginning 2 October is excluded as there were only 5 h of acoustic observations during this period.

methods of estimating range are possible. For example, if the source level of the sounds and the propagation conditions for the site are known, the range can be estimated from the level received on one hydrophone. While this index is likely to be a less effective indicator of numbers of whales passing than the number of singers, it can be measured with a simpler system and with less effort and so may be suitable for use in automated systems.

#### ESTIMATE OF POPULATION PARAMETERS.

Four parameters of the population were estimated for the period of observation: (i) total number of south-bound whales passing through the study area, based on visual observations, (ii) total number of whales passing through the study area regardless of migratory direction, based on visual observations, (iii) total number of singers passing through the study area, based on acoustic observations, and (iv) total number of singer-hours generated in the study area. Ratios of singers and singer-hours with whales seen, across the entire study period, were calculated using these estimates.

Data for each day with 5 or more hours of observation were normalised to the equivalent for a 10-h day which was considered to be a sample unit (days with less than 5h of observation

were not included in the analysis). It was assumed that the numbers of humpback whales passing Peregian Beach were unaffected by whether it was day or night, and that the numbers passing day by day varied in a random manner, apart from the broad rise and fall over the full period of migration of several months. Then our sampling could be considered to be a reasonable approximation of random sampling (Cochran, 1963). Each sample was drawn out of a population of 156 10-h units over the 65 days of observation ( $65 \times 24/10 = 156$ ).

Because of the long term rise and fall in numbers during migration (Fig. 5A,B), there are advantages in using stratified random sampling theory (Cochran, 1963). Application of this technique to surveys of this humpback whale population is discussed in Paterson et al. (1994, 2001). The following three strata were used for all estimates of acoustic and visual data: 28 August – 1 October (days 1-35), 2 October – 15 October (days 36-49), 16 October – 31 October (days 50-65).

A total of 55 visual sample units and 46 acoustic sample units were obtained out of a possible 156 units over the 65 day observation period. This includes acoustic data only for those days that had corresponding visual data (i.e. >5h

of visual observations). Nine of the days of visual observations did not have acoustic positions because the array was down (including a scheduled maintenance period from 30 September to 8 October).

The population size with 95% confidence interval is (Cochran, 1963)

$$N\bar{y}_{st} \pm tNs(\bar{y}_{st})$$

where  $N$  is the total number of units,  $\bar{y}_{st}$  is the weighted mean,  $t$  is the value of the Student's  $t$  distribution for a two-tailed value of 0.05, and  $s(\bar{y}_{st})$  is the weighted estimate of standard deviation. The value of  $t$  was determined for the effective numbers of degrees of freedom (for small sample sizes, Cochran, 1963, based on Satterthwaite, 1946)

$$n_e = \frac{(\sum g_h s_h^2)^2}{\sum \left( \frac{g_h^2 s_h^4}{n_h - 1} \right)}$$

where  $n_h$  is the number of samples for stratum  $h$ , and  $s_h^2$  the variance of the samples in each stratum. The final term  $g_h$  is given by

$$g_h = \frac{N_h(N_h - n_h)}{n_h}$$

where  $N_h$  is the total possible number of sample units in each stratum.

Daily and weekly numbers of singers and singer-hours were correlated against each other to test the strength and significance of song activity as an indicator of the number of singers using linear regression analysis (Excel, Microsoft). Singer numbers and singer-hours were also correlated with numbers of whales seen. In addition to using population estimates to calculate ratios of song activity and whales seen across the entire study period, linear regression analysis was used to calculate regression coefficients with confidence limits for daily and weekly data.

## RESULTS

**VISUAL CENSUS.** During the 65 day survey period, 529 hours of observations were made including 39 full 10-h days, 16 days with 5-10h, 5 days with some observations but <5h, and 5 days with no observations. A total of 279 pods of whales were observed travelling in both directions containing 501 whales including 43 calves (Fig. 6). Pods were tracked with 1,792 theodolite-measured positions. For pods with

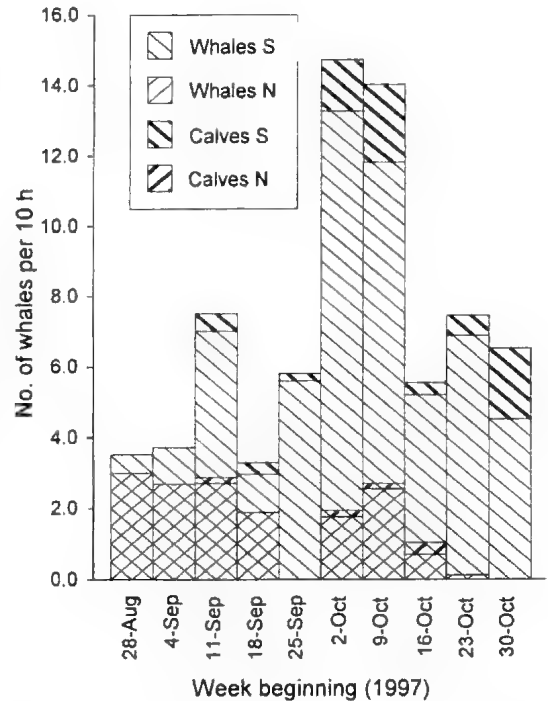


FIG. 6. Weekly numbers of visually observed humpback whales passing within 10km of Peregrine Beach. Includes all visual data regardless of whether it is matched by acoustic data.

clear migratory direction, mean pod sizes were 1.73 north-bound (s.d. = 0.69,  $n = 52$ ) and 1.97 south-bound (s.d. = 0.83,  $n = 172$ ).

The number of south-bound whales passing within 10km of Peregrine Beach between 28 August and 31 October 1997 was calculated to be  $1,148 \pm 170$  (95% confidence interval, using techniques described by Cochran, 1963). This can be expected to significantly underestimate the stock size since: we have sampled only part of the southward migration; a significant proportion of whales passes beyond 10km at Peregrine Beach; and, an unknown proportion may have been missed. An estimate of total stock passing during our limited period of observation can be made with reference to the data of Paterson et al. (1994: fig. 4) for 1992 off Point Lookout. These data show that the number of south-bound humpback whales seen passing Point Lookout between 28 August and 31 October (the period of our observations) amount to ~78% of those seen north-bound between 5 June and 31 October, the period over which their population estimate of 1,900 was made. At the annual rate of increase determined by Paterson et al. (11.7%), the

population in the northern migration of 1997 is estimated to be 3,300, so that the numbers passing between 28 August and 31 October would be 2,580. Thus, if the ratio is similar off Peregrine Beach, we would expect 2,580 whales to pass during our period of observation, 2.25 times the number estimated from our observations. Our estimate is therefore 45% of the numbers expected from the data of Paterson et al. The most likely explanation for this discrepancy is that approximately half the whales passed beyond the 10-km limit of the survey.

The estimated number of whales (regardless of migratory direction) passing through the study area between 28 August and 31 October 1997 was  $1,424 \pm 186$  (95% confidence interval).

**ACOUSTIC SURVEY.** The full array was operational for 44 full-days, 7 part-days and not operational on 14 days due to the loss of one or more hydrophones. At least one hydrophone was operational for all but 48 hours of the survey period. Approximately 380 hours of recordings were made during the observation period although some of these were made out of visual survey hours including at night. Four hundred and thirty-two hours of array monitoring coincided with visual observations yielding 124h of recordings from an estimated 48 singers that passed within 10km of the array.

Concurrent acoustic and visual observations occurred across the survey period except for the week starting 2 October when the array was undergoing maintenance. During this week only 5h of concurrent observations were made and so analyses using average weekly data exclude this period.

The accuracy of determining the range of the source decreased with distance, small errors in determining the bearings from each pair of buoys resulting in progressively larger errors in range as range increased. Calibration results indicated that acoustic positions suffered mean range errors increasing from approximately 5% of range at 2km to 10% at 10km and 18% at 20km. These errors were for single positions using a single cue. When positions were calculated for singers, however, impossible positions based on the course and speed of the singer could be discarded allowing some improvement in accuracy. These results are consistent with other studies using similar methods that have found reasonably accurate results at ranges of 4-10 times the array dimensions (Watkins & Schevill, 1972;

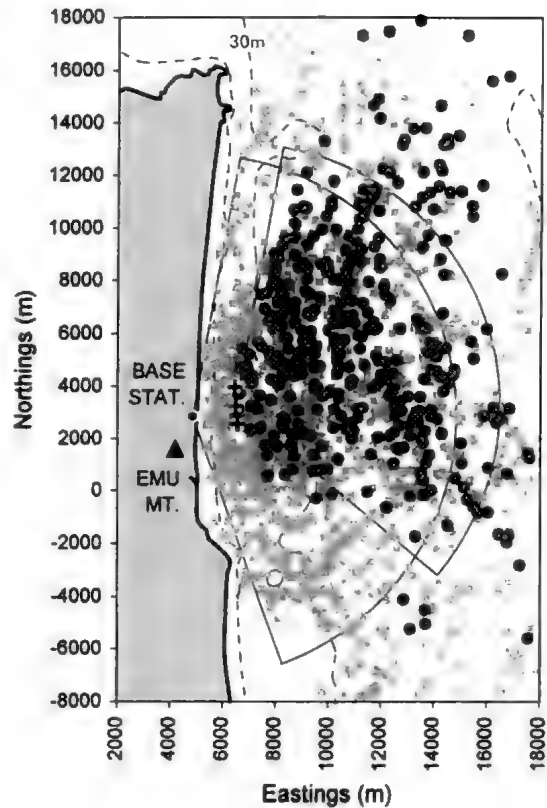


FIG. 7. Distribution of all visual (grey square) and acoustic (black dot) positions from the study. Singers could not be tracked through the southern portion of the study area due to severe attenuation of song sounds received at the array. Although whales were seen traversing the study area in less than 10m of water, singers were not recorded singing in waters of <20m depth.

Cummings & Holliday, 1985; Frankel et al., 1995; Clark & Ellison, 2000).

Empirical observations and calibration studies showed that propagation of sound throughout the area was not uniform (Fig. 7). Sounds from tracked singers suffered sudden and severe attenuation when entering the southern part of the study area, particularly on the southernmost buoy, and so were not able to be tracked further and were often soon lost altogether on all hydrophones. This acoustic shadow was confirmed by the bulb-imploding calibration experiments and appeared to be due to the presence of a shoal south of the array. Another array 'blind spot' existed to the north of the array. Here the singers could be heard but range determination was prone to large errors within  $\sim 10^\circ$  of the end-fire

axis of the array (line through the hydrophones) due to the increased sensitivity of the estimates of bearings to small errors in the measured time-of-arrival-differences, as well as the increasingly acute angles of intersection of the hyperbolae. The arc of effective array function, therefore, extended from  $10^\circ$  to  $130^\circ$  (Fig. 2).

Total singers and singer-hours in the useable portion of the study area during the study period were  $180 \pm 50$  and  $418 \pm 106$  (95% confidence interval) respectively. Daily and mean weekly song activity fluctuated throughout the migration in a manner that reflected the numbers of singers tracked through the study area (Fig. 8A,B). Correlation of daily singer-hours against singers gave a correlation coefficient  $r = 0.86$  ( $P < 0.01$ ,  $n = 44$ ) while correlation of mean weekly singer-hours against singers gave a correlation coefficient  $r = 0.94$  ( $P < 0.01$ ,  $n = 9$ ). The singer-hour index was therefore a reliable and accurate indicator of the number of singers passing through the area.

Although whales were seen traversing the study area in less than 10m of water, singers were not recorded singing in waters of  $<20$ m depth (the depth at the array) (Fig. 7).

**COMPARISON OF VISUAL AND ACOUSTIC RESULTS.** Numbers of singers and singer-hours also fluctuated throughout the migration in a manner similar to the numbers of whales seen (Fig. 5A,B). Correlation analysis for daily averages gave correlation coefficients  $r = 0.68$  and  $0.64$  for singers and singer-hours, respectively ( $P < 0.01$ ,  $n = 46$ ), and for weekly

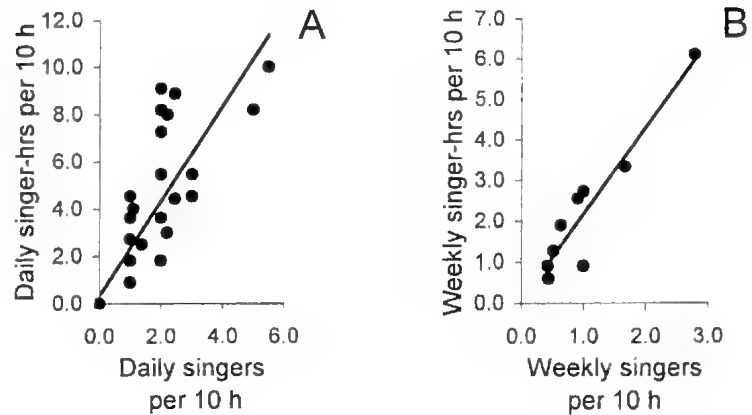


FIG. 8. Linear regression of daily and weekly numbers of singers against numbers of singer-hours of song activity. A, daily counts of singers and singer-hours normalised for a 10-h day; B, weekly averages of daily normalised counts. Only days with more than 5h of matching visual data are included.

averages  $0.79$  and  $0.89$ , respectively ( $P < 0.01$ ,  $n = 10$ ).

Ratios of singers and singer-hours to whales seen for daily and weekly averages were determined by linear regression analysis (Fig. 9A-D, Table 1). In all cases, regression coefficients were calculated for both regression lines of best-fit and for regression lines passing through the origin (as there should have been no singers or song if there were no whales). Ratios of singers and singer-hours to whales seen were also calculated using the calculated full-survey population parameters (Table 1).

These results effectively give a range of ratios calculated from data averaged over three time frames — daily, weekly, and the entire 65-day study period. Daily results, with their greater spread and sample size, probably provide the most accurate measure of the relationships between acoustic activity and whales seen, reflected in their narrower confidence intervals. Also daily coefficients of regression are less affected by regression through the origin than

TABLE 1. Ratios and regression coefficients ( $b$ ) with 95% confidence intervals of numbers of singers tracked and numbers of singer-hours to numbers of whales seen over three different time scales. No confidence intervals were calculated for the full survey ratios.

	Regression of daily results				Regression of weekly mean results				Full survey ratio
	Best-fit		Through origin		Best-fit		Through origin		
	<i>b</i>	95% CI	<i>b</i>	95% CI	<i>b</i>	95% CI	<i>b</i>	95% CI	
No. of singers vs no. of whales seen	0.137	± 0.045	0.127	± 0.027	0.138	± 0.087	0.131	± 0.035	0.126
No. of singer-hours vs no. of whales seen	0.299	± 0.110	0.288	± 0.065	0.467	± 0.199	0.345	± 0.093	0.294

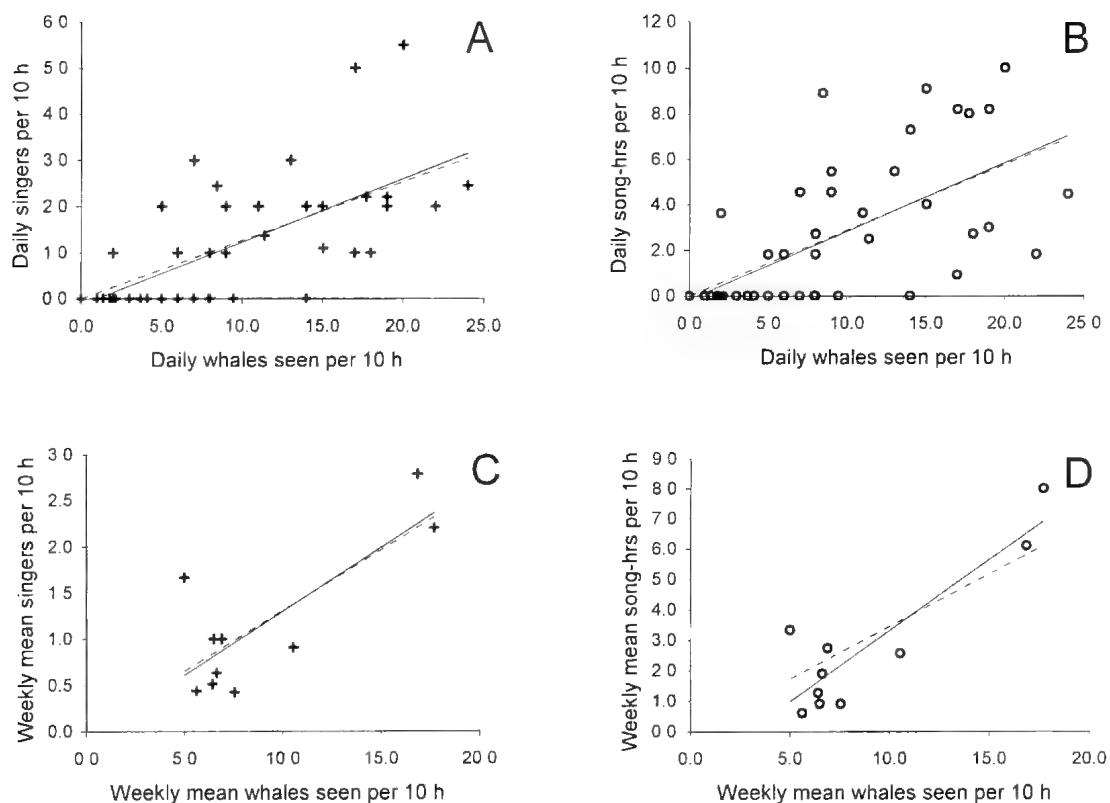


FIG. 9. Linear regression of daily and weekly numbers of whales seen against numbers of singers and singer-hours heard; solid lines are regression lines of best fit, dotted lines pass through the origin. A, daily singers and whales; B, daily singer-hours and whales; C, weekly singers and whales; D, weekly singer-hours and whales. All counts have been normalised to a 10h day. All figures are based on days with both visual and acoustic data.

weekly ones, particularly in terms of confidence limits, further suggesting their suitability as the best model used.

Although confidence limits were not calculated for population parameter-based ratios, the population parameter confidence limits suggest that they would be greater than those from the linear regression models. Unlike data used in the regression analyses, the population parameters calculated also include visual data not paired with acoustic data as the primary aim was to generate population parameters rather than ratios. Despite these differences in methodologies, the results of all analyses are in broad agreement, indicating a ratio of singers to whales of approximately 0.13 and singer-hours to whales of approximately 0.30 (Table 1).

Measures of the number of singers and total number of whales are effectively counts of the numbers of individuals passing the observation

point. The results should be largely independent of the size of the observation sectors so long as there is a high probability of an individual being detected when passing through the sectors. This was the case, since whales tended to move through the full arc of the sectors, allowing individuals to be detected a number of times, both visually and acoustically. Hence, the fact that the area of the visual survey was about 25% larger than that of the acoustic survey is not expected to have significantly affected the comparison of the number of singers passing with the total number of whales passing.

On the other hand, estimates of singer-hours are likely to be proportional to the area of observation, since the index depends on the number of singers in the area at the time of measurement, and this would be proportional to the area if the density of singers were uniform or random. Hence this is a hybrid index depending

on both numbers of whales passing and area of observation. The relationship between number of whales passing and the singer-hour index would need to be determined for the particular set of conditions of observation and is not applicable generally. In this study, increasing the ratio of singer-hours to whales seen by 25% would be one way to compensate for the mismatch in the visual and acoustic availability of whales.

### DISCUSSION

The acoustic and visual surveys were made in a region where many passing whales could be expected to be seen within the 10km range selected. The good correlations between number of singers, the level of singing activity, and the numbers of whales seen show that acoustics can provide an effective index of relative abundance and an estimate of absolute abundance. Relationships between the number of singers and the total number of whales and between singer-hours and the number of whales are likely to vary with time of year and location and, particularly in the case of the singer-hour index, with the conditions of observation. Thus factors relating acoustic observations to abundance estimates are not universally applicable and will need to be determined for the particular time, place and conditions of observation (although, to some extent, this is also required in relating visual observations to abundance). Estimates of relative abundance would not require these factors to be determined if it is reasonable to expect them to be constant over the period of study. For example, a rate of increase over a number of years could be determined directly from the acoustic index if the observations were made at the same location and at the same time of year.

The factor relating the number of singers to the abundance depends on the proportion of whales singing, however this may vary with changes in behaviour through the breeding season and with variations in the proportion of mature males. Cato et al. (2001) found that the proportion of whales singing off the Australian east coast during the northward migration was less than half that of the southward migration, and there is evidence of variation in the amount of singing between night and day although whether this is due to more whales singing or individuals singing for longer periods is unknown (Au et al., 2000). With regards to the proportion of mature males, the east Australian population has a high rate of increase (Bryden, 1985; Paterson & Paterson, 1989; Bryden et al., 1990, 1996; Paterson et al., 1994,

2001) and so is expected to contain relatively few mature males (Best, 1993), although this may be offset to some extent by the apparent sex-bias towards males in the migratory population (Brown et al., 1995). The proportion of mature males in the population also varies during each migration due to some stratification within the migratory stream of different age, sex and reproductive classes (Chittleborough, 1965; Dawbin, 1966, 1997). The proportion of whales singing may also be different in open ocean migration to that near shore. Determination of the proportion singing over a wide range of conditions is necessary and may allow this method to be widely used.

The measure of singer-hours is less robust, since it depends also on the duration of singing and transit time of individuals, and the area of observation. In this study we have used an estimate of singer-hours based on 10min samples hourly during daylight hours as the basis of such an index, but other sampling regimes are possible and may be preferred depending on the circumstances and resources of the study. In any case, it will need to be determined for the particular set of conditions for each study. The advantage of such an index, however, is that it requires significantly less observation and analysis effort than determining the number of singers. More effort is required to 'calibrate' an index for the particular conditions, but this may be more than compensated by the substantially larger data sets that can be analysed.

Any estimate of abundance requires a determination of the spatial or temporal density of animals so that the result can be extrapolated to their full spatial or temporal range. In this study, positions of singers were determined using the time of arrival differences on the three accurately positioned hydrophones, to limit the estimate to those singers within the sector. This required substantial effort and simpler methods could be used to estimate the singer-hour index (or other song activity index), since this does not require actual location of the sources, only that they are within a chosen distance of the hydrophones. For example, distances of sources from a single hydrophone can be estimated from the received levels of the sounds if the source levels and propagation conditions are known. Propagation characteristics vary widely with location and time, however, and source levels may also vary. The results would have a larger uncertainty than those obtained by localisation, but need only a single hydrophone system and much less analysis



and would be particularly suitable for automated systems or deployed packages where periodic sampling was used. Cato (1998) discusses the use of two hydrophones to determine ranges of underwater biological sound sources. In this case, the positions of the hydrophones did not need to be known and was more accurate than a single hydrophone, but still required a knowledge of propagation loss to minimise errors. The use of towed arrays in ship-based surveys may also allow positioning of whales with ambiguity, though range of detection would be less than that of fixed systems due to higher system noise (e.g. Gillespie, 1997; Clark & Fristrup, 1997). It should be noted that an estimate based on the number of singers audible without determining their distances would be quite unreliable, because of the wide range of audibility due to the large variation in ocean background noise that is expected.

This study demonstrates the importance of the effect of the acoustics of the environment, particularly in shallow water, in acoustic surveying. A shoal caused an acoustic shadow to the south and limited that area over which whales could be tracked (Fig. 7). The use of the singers themselves as a calibration tool is also demonstrated — the song could be heard to attenuate rapidly as they were followed acoustically and visually into this area.

The distribution of whale numbers over the period of the visual survey resembles closely those of previous southward migration surveys off southeast Queensland (Chittleborough, 1965; Paterson et al., 1994) demonstrating that the pattern of southward migration within 10km of Peregrine Beach is representative of the migration. The results indicate, however, that a substantially larger proportion of whales pass beyond 10km of land than off Point Lookout on North Stradbroke I. The total number of humpback whales seen within 10km was about half the number that would be expected off Point Lookout between the same dates. We saw many whales beyond 10km whereas aerial surveys have shown that only 5% of whales pass Point Lookout beyond 10km (Bryden, 1985). Humpback whale migration paths would be expected to converge around Point Lookout, since this is the most easterly point in the region (Fig. 1). The effect would be a concentration of whales closer to Point Lookout than to the mainland to the north or south (Bryden, 1985; Paterson, 1991). Peregrine Beach is ~100km north of Point Lookout and

~45km west, so that a greater dispersal of whales from shore might be expected there.

This greater spread of humpback whales also suggests that within the 10km limit of this study, a greater proportion pass further out than at Point Lookout. While Bryden et al. (1996) concluded that around 10–14% of pods were missed during northward migrations at Point Lookout, Findlay & Best (1996a) found that, at ranges of 6–10km, 40–50% of pods were missed at Cape Vidal, South Africa. The offshore distribution of whales at Peregrine Beach may therefore lead to a higher proportion of missed whales than from Point Lookout, especially since a significant proportion may be new-born calves (about 10% of humpback whales observed off Point Lookout in the southward migration: Paterson & Paterson, 1989; Paterson et al., 1994). This survey does not attempt to correct for whales missed within 10km, but these results suggest that part of the difference with that expected from the Point Lookout surveys is due to a greater proportion of whales missed between 6–10km. However, it seems likely that most of the difference is due to the greater proportion of passing whales passing >10km off Peregrine Beach.

The site of this study was chosen to be an area where visual observation is particularly effective, to provide 'ground-truthing' of acoustic methods of surveying. While this study demonstrates that acoustic methods could be effective as stand-alone surveys, it is unlikely that acoustic surveys will be conducted in preference to land-based visual surveys where these are possible. The main application of acoustic surveys would be to regions where visual surveying is limited, such as the open ocean, where acoustic systems could be left to record for months at a time. Acoustics may also be useful in conjunction with visual surveying by providing a second, independent method of counting whales to improve the reliability of observations.

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## APPENDIX

### DETERMINATION OF THE RANGE TO A WHALE USING THEODOLITE ANGLES

This study uses a technique derived from basic trigonometry to calculate the distance of a whale from the observation point, allowing for the curvature of the earth and refraction.

The angular effect of refraction is expressed as a *coefficient of refraction*,  $k$ , the ratio of the difference between the true and apparent angles to the whale,  $r$ , and the angle subtended at the centre of the earth,  $\theta$ , i.e.  $k = r/\theta$ . The value of  $k$  over water is generally accepted as being 0.08 (Ingham, 1975) and the appropriateness of this value was confirmed empirically during our calibration experiments. As  $k$  is theoretically applicable to the correct angle  $\theta$ , an iterative process is required where, for each iteration, a correction to the apparent angle  $\alpha$  is calculated based on the previous iteration's  $\theta$ . A series of six iterations was sufficient to calculate a true value of  $\alpha$  to less than one second of arc, exceeding the limitations of the theodolites used.

In Appendix Fig. 1,  $R$  = radius of the earth (6,372km at 27°S),  $H$  = height of theodolite

above sea level,  $D$  = distance along the surface of the sea from the base of the observation point to the whale, and  $\alpha$  = the azimuth (vertical angle to the object). Since in any triangle the ratios of the sines of the internal angles to the lengths of the opposite sides are equal,

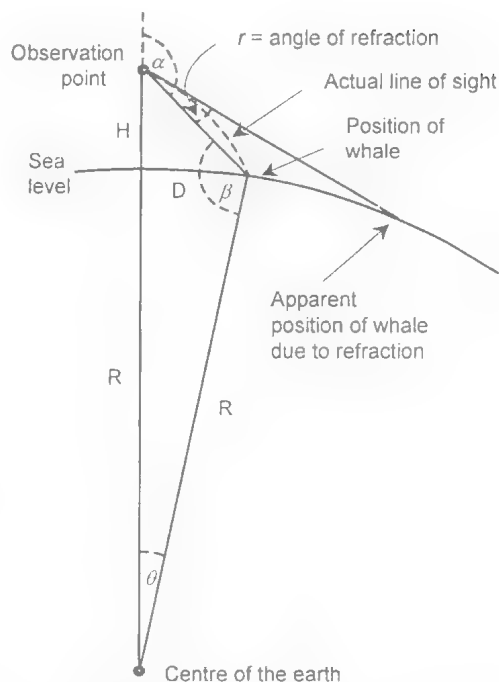
$$\frac{\sin \alpha'}{R} = \frac{\sin \beta}{R + H} \quad \text{where } \alpha' = 180 - \alpha$$

$$\text{so that } \beta' = \sin^{-1} \left( \frac{\sin \alpha (R + H)}{R} \right) \quad \text{where } \beta' = 180 - \beta$$

$$\begin{aligned} \text{Now } \theta &= 180 - \alpha' - \beta \\ &= \alpha + \beta' - 180 \end{aligned}$$

Therefore

$$D = R\theta \frac{\pi}{180} = \frac{R\pi}{180} \left( \alpha + \sin^{-1} \left( \frac{\sin \alpha (R + H)}{R} \right) - 180 \right)$$



APPENDIX FIG. 1. Geometry of the use of a land-based theodolite to measure the range of objects at sea.

**HUMPBAC WHALES IN THE MAGELLAN STRAIT, CHILE. (POSTER)** The humpback whale (*Megaptera novaeangliae*) population in southeastern Pacific breeds in Colombian coastal waters in the austral winter and feeds in Antarctic Peninsula during summer. Between these migratory end points little is known. Surveys along Chilean Patagonian channels and the Magellan Strait from 1997 to 2000 showed seasonal presence of humpback whales from spring to fall. We investigated humpback whales in the Magellan Strait and Otway Sound to examine if the area represents a regular feeding ground or a migratory route for the species. Sixteen dedicated surveys of 2 to 5 days were carried out, spanning 46 days in 14 different months from January 1999 to June 2000 to determine behavior, residence and site fidelity of individual humpback whales. Research was undertaken by direct observation of whales and by photoidentification. A total of 23 individuals of 76 humpback whale groups were identified and catalogued. Residence was established during the austral summer from seven individuals: one whale stayed for a five-month interval, three for 3 months and three during a two-month interval. Two

whales sighted in 1999 returned to the area in 2000. Feeding activities were both observed and suggested by co-occurrence of sea lions and marine birds with whales in foraging behaviours. These preliminary results support the hypothesis that the study area is a regular feeding ground for humpback whales. Historical records also show that the area has been occupied by whales since the Fifteenth Century, providing additional evidence that the place has been a traditional and regular feeding site. Comparisons looking for matches in photographs with individual humpback whales catalogued from Colombia and Antarctic Peninsula are in progress. The analysis described here represents a preliminary framework for a planned assessment of humpback whales in the Patagonia.

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**STOCK STRUCTURE IN 'AUSTRALIAN' HUMPBAC WHALES REVISITED. (ABSTRACT)** Humpback whales (*Megaptera novaeangliae*) that migrate from Antarctic waters along the east and west coasts of Australia during the winter months are thought to comprise distinct stocks. Support for this segregated migration has come primarily from genetic analyses of female lineages through mitochondrial DNA, where a small but statistically significant difference in haplotype frequencies has been shown. However, results for biparentally inherited genes do not support the conclusion of separate stocks because estimates of genetic differentiation at nuclear microsatellite loci between whales from the east and west coast are not significantly different to zero. This finding reflects similar studies from the Northern Hemisphere and suggests that stock

boundaries be reappraised. The results of other research also alludes to weaker population structure than thought previously in that only about half the presumed female population on the east coast makes the northward migration each year. Estimates of population size from direct whale counts should consider all regional migration paths and fluctuations in numbers on any one path.

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**HUMPBAC WHALES OF THE ARCHIPIELAGO REVILLAGIGEDO, PACIFICO MEXICANO, 1996-2000: GENERAL POPULATION CHARACTERISTICS. (ABSTRACT)** The Archipiélago Revillagigedo consists of four small volcanic islands 375-575 miles west of mainland Mexico, and 250 miles south of the Baja Peninsula. Photographic identification studies of humpback whales (*Megaptera novaeangliae*) wintering at Isla Socorro, the largest island, were conducted with varying effort (0.5 to 3 months) from 1986 to 1995. In 1996 we began a long-term detailed study with 2.5-3 month long field seasons. Preliminary results have confirmed the unusually high resighting rates previously observed. From 1996-1999 we identified 573 individuals at Isla Socorro, with 28.7% sighted in more than one year. An average of 49.0% of whales sighted in a season were sighted on more than one day during that season. Of the 180 individuals identified in 1999, 47.2% had been sighted in at least one of the previous three years. The sex of 198 individual whales (48 females, 150 males) was determined by behaviour. Males had greater maximum and

average intervals between first and last sightings within a season (79 and 19.1 days respectively) than females (50 and 15.2 days). In 1998 and 1999 we also surveyed at Isla Clarion (200 miles west of Isla Socorro) and 60.6% of the 127 whales identified there also were sighted at Isla Socorro during 1996-1999. We observed 31 within-season transits between islands, primarily by males. Data from the 2000 field season at both islands will be incorporated into the above analyses, and mark-recapture population estimates will be made using the entire five year database.

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# QUALITATIVE AND QUANTITATIVE ANALYSES OF THE SONG OF THE EAST AUSTRALIAN POPULATION OF HUMPBACK WHALES

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Macknight, F.L., Cato, D.H., Noad, M.J. & Grigg, G.C. 2001 12 31: Qualitative and quantitative analyses of the song of the east Australian population of humpback whales. *Memoirs of the Queensland Museum* 47(2): 525-537. Brisbane. ISSN 0079-8835.

Humpback whales produce a complex sequence of vocalisations, called songs, while on migration paths and breeding grounds. While its function remains unclear, the association between song and its production during the breeding season has led to the hypothesis that song may be an acoustic display used by males to attract potential mates and repel rival males. If so, significant differences in the song between singers might be expected. Here we describe the structure of the song off east Australia in 1998 and present a quantitative comparison of the acoustical characteristics of two sound types between six individual singers to determine the extent that these provided discrimination between individuals. The song was found to consist of five themes produced in a fixed order, consistent with other observations of humpback whale song. Multivariate and univariate tests showed significant measurable differences between individuals for all acoustical parameters included in the analysis. However, for any parameter, the differences were accounted for by one or two individuals and there was no observable pattern or consistent differences between individuals. Canonical analysis showed substantial overlap between clusters suggesting poor discrimination between individuals. The frequency of different units of the same sound type varied by less than two semi-tones for an individual and no more than three semi-tones between individuals, suggesting that humpback whales have a well refined perception of pitch. We conclude that while there were differences between individuals in the characteristics of the two sounds analysed, these did not provide useful discrimination between individuals. □ *Humpback whale, song structure, Australia.*

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Humpback whales, *Megaptera novaeangliae*, migrate annually from high latitude feeding grounds in summer to low latitude tropical waters to breed and calve during winter (Chittleborough, 1965). During this migration humpback whales produce a complex sequence of vocalisations known as 'song' (Payne & McVay, 1971).

The function of song remains unclear. There is evidence that only male humpback whales sing (Glockner, 1983; Baker & Herman, 1984) and singing appears to be confined to the migration pathway and breeding grounds. This relationship with the breeding season has given rise to the hypothesis that song is a powerful acoustic display for attracting mates (Tyack, 1981; Winn & Winn, 1978; Frankel, 1994). However, other explanations include a spacing function among males (Frankel et al., 1994) and a means of establishing a dominance hierarchy (Darling et al., 1983). Multiple use of acoustic displays such as song is not uncommon and is well documented in many bird species (Catchpole & Slater, 1995).

Hypotheses that female humpback whales obtain information about singing males via songs, or that males assess the fitness of other males through song are 'only viable if songs exhibit reliably perceivable inter-individual differences' (Tyack, 1981). Studies of odontocetes confirmed the existence of individual-specific, stereotyped whistles, called signature whistles, and these have been implicated in direction communication between individual bottlenose dolphins (Caldwell et al., 1990; Tavorla, 1983).

The evolution of song over time would tend to work against the development of individual-specific information, at least in song pattern and structure. A more reliable identifier may be in acoustical characteristics of sound types. Research into the acoustical properties of humpback whale song has focused primarily on qualifying the characteristics of sound types, describing the overall pattern of the song and documenting song evolution across years (Payne et al., 1983; Guinee et al., 1983; Payne & Payne, 1985; Mednis, 1992). Inter-individual variability in the



acoustical characteristics of sound types, although identified, has been not been extensively researched. Payne & Payne (1985) noted that inter- and intra-individual variability existed but variation between songs of consecutive years was much greater. Hafner et al. (1979) suggested that individual-specific information could be encoded within the 'cry' component of songs. However, comparisons of cries were obtained from only five whales over a three-year period. Frankel (1994) measured four parameters for each of six sound types and demonstrated significant differences between whales for each of the variables. He concluded that individual-specific information could be contained within sound types but did not investigate further.

If there is significant variability in the acoustical characteristics of the same sound type sung by different individuals, and this variability is consistent within individuals, individual-specific information may be encoded within the song. Further, such information might be used by females in selecting males for reproduction.

Here we qualitatively describe the structure and pattern of the song and conduct a detailed quantitative analysis of the acoustical characteristics of selected sound types to determine if these contain information that allows discrimination between individuals. An understanding of the characteristics of humpback whale song and how song varies between individuals will augment current knowledge pertaining to song function, the role of song in the reproductive process, and may provide a clearer understanding of the species' social structure.

#### METHODS

**STUDY SITE.** Point Lookout, North Stradbroke Island (27°26'S, 153°33'E) is situated ~18km off the southeast Queensland coast (Fig. 1). During winter humpback whales migrate along the coastline with most passing within 10km of the shore at Point Lookout (Paterson, 1991). Recordings of humpback whale song were obtained from 20th to 31st July 1998. This period was chosen to avoid the confusion from multiple singers evident closer to the peak of the northward migration which occurs late June to early August (Paterson et al., 1994; Bryden et al., 1990; Brown et al., 1995).

**RECORDING EQUIPMENT.** Recordings were obtained using a bottom-mounted buoy developed by the Defence Science and Technology Organisation, Sydney, with some modifications

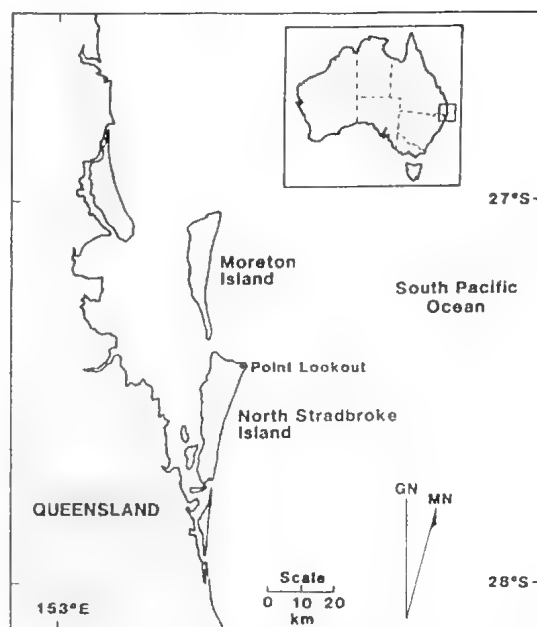


FIG. 1. Study site. Hydrophone-buoy was positioned ~3km offshore, east of Point Lookout.

specified for this project. The hydrophone-buoy was a spar buoy design, constructed of pressure PVC piping supported by a fibreglass torus float and maintained in position by an anchor on the sea floor. The buoy was anchored ~3km offshore in 30m of water.

The hydrophone was a GEC marconi SH101X connected to an RANRL pre-amplifier and housed in a separate PVC canister underwater to avoid electromagnetic interference and suspended at a depth of 17m. The pre-amplifier had a 40dB gain and 1M $\Omega$  input impedance. Frequency response of the system was 30Hz-14,000Hz.

The signal was transmitted using VHF and received by a vertically polarised YAGI antenna connected directly to a 4-channel VHF radio receiver (type 8101). Recordings were made directly to a Sony TCD-D7 Digital Audio Tape recorder (DAT). The received signals also ran directly into a desktop computer for real time analysis using Spectrogram 4.2.10 (developed by R.S. Horne).

**DEFINING AN INDIVIDUAL.** No information on sex or age of individuals was obtained and it was not possible to positively identify individual whales. Therefore, the following assumptions and guidelines apply. 1) Singers recorded on different days were different individuals. Recordings were obtained from the migration

pathway therefore individuals were mobile and did not remain within acoustic range of the hydrophone for extended periods. Observations have shown that whales are clearly in transit as they pass Stradbroke Island (Paterson, 1984; Cato, 1984) and singers have been observed travelling at speeds greater than 1 km per hour (Frankel, 1994; Helweg et al., 1992).

2) All recordings used in the analysis are unbroken, i.e. the recording of an 'individual' is continuous and there is no break or pause in singing (or recording).

3) As humpback whale song changes over time (Payne et al., 1983; Guinea et al., 1983; Cato, 1991) if any observed differences were to be associated with inter-individual variability, recordings must be considered contemporaneous, i.e. separated in time by no more than a few weeks (Cato, 1991). In this study the maximum separation time between recordings analysed is nine days. As changes in the song over such a short interval have been found to be negligible (Payne & Payne, 1985; Cato, 1991; Frankel, 1994; Helweg et al. 1998), it is unlikely comparisons were confounded by temporal changes.

Each whale was given an identification number according to year/month/day/recording number, e.g. individual 807223 was recorded in 1998 on July 22 and was the 3rd recording made on that day.

**ANALYSIS. Spectrographic Analysis.** Sonagrams were created using the PC-based sound analysis software Spectrogram (v. 4.2.10). Initial inspection of sonagrams indicated that the majority of sound energy lay below 4 kHz. Thus, recordings were digitised with 16-bit resolution at a sampling rate of 5.5 kHz. Sonagrams were generated with a Fast Fourier Transform (FFT) of 1024 points yielding a 5.4 Hz frequency resolution and 186 msec time resolution.

**Pattern Analysis.** Descriptive names were used to identify particular sound types, e.g. 'growl', 'down moan', 'high cry', 'bellow'. Once each sound type had been assigned a label it was possible to identify the order and timing of the phrases, themes and subsequently the pattern of the song for each individual using a combination of aural and spectrographic analysis.

**Statistical Analysis.** We identified two sound types on which to base a quantitative statistical analysis of variability. These sounds were chosen as initial aural examination suggested that they were quite variable and because the spectrographic parameters could be measured with little ambiguity.

Sound type 1 was a narrow-band frequency modulated sound with associated harmonics. Initial analysis demonstrated that it was possible to obtain a reasonable approximation of the frequency contour by measuring the following variables: start frequency (Hz); end frequency (Hz); number of inflection points; frequency (Hz) and time (ms) at each inflection point; frequency range, expressed as the ratio of the maximum to minimum frequencies (Hz); duration (ms). The ratio of frequencies between the start and the first inflection point and at the first and second inflection points were also calculated. An inflection point is defined as a change in the slope of the frequency contour from positive to negative or vice-versa. Time and frequency were recorded at the point where the slope of the frequency contour moved through zero, or as close to this point as was possible.

Sound type 2 was a short, narrow-band sound with little frequency contouring. Each sound unit was divided into four equal sections and the following variables were measured: start frequency (Hz); frequency at 1/4 point (Hz); frequency at midpoint (Hz); frequency at 3/4 point (Hz); duration (msec); frequency range (Hz). We used ratios rather than absolute differences in frequencies because studies of hearing suggest that the perception of frequency can be related to a logarithmic scale of frequency, i.e. perception is of relative rather than of absolute frequency (Yost, 1994).

For both sound types, the sound units measured were selected from the same part of the song, being the first occurrence of the theme after a surfacing, as determined by the audible drop in level associated with surfacing behaviour (Cato, 1991). Generally, the units measured were the first occurrence of the sound type for each phrase, however, as some sound units could not be measured accurately, due to interference masking some portion of the sound, the sound unit from the phrase immediately following was measured. Both sound types analysed came from the same song.

**Univariate and Multivariate Statistical Analysis.** To investigate differences between individuals, based on all variables, a 1-way multivariate analysis of variance (MANOVA) was performed. Post hoc tests were examined to identify which individuals were significantly different according to each variable. Kruskal-Wallis ANOVA's were run for each variable to identify specific dependent variables that contributed to the significant overall effect.

*Canonical Discriminant Function Analysis.* To determine whether individuals could be discriminated statistically based on a set of given variables, a canonical discriminant function analysis (CDA) was run.

## RESULTS

The survey period yielded 68 hours of recordings across a 12-day period. Continuous recordings, of a reasonable length (minimum of 9 complete song cycles) and good signal to noise ratio, were obtained for 7 individuals. A total of 25hr of recordings from 7 individuals was analysed to describe the song structure.

**DESCRIPTION OF SOUND TYPES.** Frequencies of all sound types (including harmonics) were in the range of 50Hz-6000Hz which is ~7 octaves. Nine distinct sound units were identified which were grouped into five themes. Sound types varied from acoustically simple to complex and were classified into four broad categories (Table 1). Each category is described by its frequency range, fundamental frequency and duration. The lowest in frequency were the 'growl' and 'bwop' sound units and the highest frequency units were the 'squeak' and 'high cry' (Table 1).

**DESCRIPTION OF SONG PATTERN.** *Phrase and Theme Structure.* The phrase structure, including order of occurrence and number of occurrences of each sound unit is presented in Table 2. Phrases contained either two or three

sound types. These were grouped into 5 themes: A-E. Sub-themes were identified by the number of occurrences of the second sound type and/or the presence of a third sound type. All themes except theme E had sub-themes. However, only sub-theme Bs is included in the table as this was the only sub-theme which incorporated a 'new' sound. The order of the sound units within each phrase was fixed and occurred invariantly, however the grunts in theme A and D were not present in all phrases.

Theme A. Arbitrarily designated as the start of the song as it was usually the first theme sung after the attenuation (indicative of when the individual moved to the surface to breathe). Phrase length was determined by the number of sound units within the theme. Mean duration = 12.84sec ( $\pm 2.70$ SD;  $n = 63$ ) (Fig. 2).

Theme B. The start was signalled by a series of 2-3 'high cries', a truncated 'transitional phrase' (Payne & McVay, 1971), with a mean duration of 4.98sec ( $\pm 0.51$ SD;  $n = 63$ ). All subsequent phrases began with a single 'modulated bellow', followed by 1-3 'high cries' (Fig. 3). The interval between the 'high cries' and the 'modulated bellow' was longer (1.6sec) than the interval between the 'modulated bellow' and 'high cries' (1.0sec). Therefore, we identified the start of each phrase as beginning with the 'modulated

TABLE 1. Classification of sound units into sound type categories and description of temporal and spectral characteristics. \* = frequency range includes harmonics obtained from good SNR recordings.

Sound Type	Frequency Range *(Hz)	Duration (sec)	Fundamental Freq. (Hz)
<b>Harmonic</b>			
Downmoan	120 - 4000	3.0 - 4.6	120 - 200
Modulated bellow	200 - 4000	0.9 - 1.5	190 - 520
High cry	450 - 6000	0.4 - 1.5	450 - 2000
Downsweep	100 - 4000	0.5 - 1.5	100 - 425
<b>Broadband Continuous Sounds</b>			
Growl	100 - 1700	0.8 - 1.2	
<b>Broadband Pulsative</b>			
Grunt	160 - 1700	0.08 - 0.16	166 - 210
Squeaks	780 - 4500		
<b>Complex</b>			
Bwop	60 - 2000	0.1 - 0.4	60 - 115
Uprill - growltrill - trill	200 - 3000	2.6 - 3.0	200 - 350 350 - 1000

TABLE 2. Phrase and theme structure. Sound units in order of occurrence and number of occurrences for each phrase and theme. \* = minimum number of occurrences. As individuals usually surface during this theme it was not possible to record all occurrences due to attenuation of the sound. # = high cries present only at start of the theme. Each subsequent phrase began with the modulated bellow followed by high cries.

Theme	Sound Units in Order of Occurrence (phrase)	No. of Occurrences of Sound Unit (per phrase)	No. of Occurrences of Phrase (per theme)
A	Downmoan Growl Grunt	1 1-2 3-12	4-13 *
B	High cry # Modulated bellow High cry	2-3 1 2-3	8-14
Bs	Modulated bellow Squeaks	1 4-6	3-6
E	Downsweep Squeaks	2 4-8	1-5
C	Downsweep Bwop	1-2 1-3	9-32
D	Uprill Growl Grunt	1 1-2 3-12	1-22

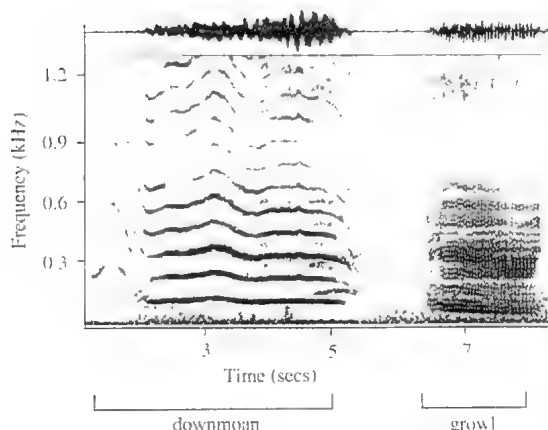


FIG. 2. Sonagram of phrase structure of theme A, comprising three sound types: 'downmoan', 'growl' and 'grunt train'. 'Grunt train' was not present in all repetitions and is omitted in this phrase. Sampling rate = 5.5kHz, FFT = 1024 pts.

bellow'. Three sub-themes were identified and defined by the number of occurrences of the 'high cry'. Sub-theme 4 (Bs) comprised the modulated bellow and a series of squeaks and was repeated between 3-6 times before the singer moved on to the next theme (Fig 3).

Theme E. Appears to be a transitional theme containing one sound type from the preceding theme (B) and one from the following theme (C). However, unlike a single transitional theme, the phrase is repeated 1-5 times which is the defining feature of a theme. Mean phrase duration was 7.76sec (SE  $\pm$  0.59;  $n$  = 63) (Fig. 4).

Theme C. An evolving theme with a systematic change in the duration and frequency range of both sound types (Fig. 5). The 'downsweep' showed some variation in acoustic character depending on the position of the sound unit within the theme. There was a gradual change in the frequency range, frequency contour and duration of the sound unit as the theme progressed. In the first phrase the 'downsweep' had a mean duration = 0.5sec ( $\pm$  0.47SD;  $n$  = 63) and the final occurrence had a mean duration = 1.5sec ( $\pm$  0.76SD;  $n$  = 63). 'Downsweeps' occurring early in the theme had an initial rise before falling with a frequency range of 120Hz-240Hz. As the theme progressed the frequency contour flattened and became a level moan with a frequency range between 100Hz-145Hz.

The 'bwop' also exhibited similar variation in acoustic characteristics depending on the position. Duration of 'bwops' at the beginning of the theme

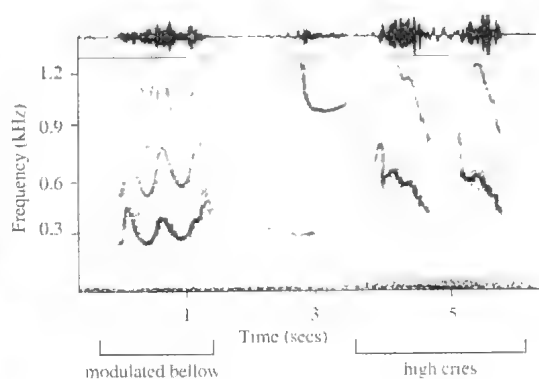


FIG. 3. Sonagram of phrase structure of theme B, comprising two sound types: 'modulated bellow' and 'high cries'. Number of 'high cries' varied from 1-3 throughout the theme. Sampling rate = 5.5kHz, FFT = 1024 pts.

was approximately 0.24sec with a fundamental frequency contour of  $\sim$ 130Hz. As the theme progressed the sound type lengthened to 0.5sec and the fundamental frequency decreased to  $\sim$ 40Hz (Fig. 5). Three sub-themes were identified defined by the number of occurrences of the 'bwop' which varied between 1 and 3.

Theme D. Each theme consisted of 1-22 phrases. Mean duration of the phrase was 11.4sec ( $\pm$  1.69SD;  $n$  = 63) (Fig. 6).

*Song Structure.* The five themes occurred in the order A-B-E-C-D. Average song length was 7.99min ( $\pm$  2.61SD;  $n$  = 115). Maximum song length was 12.93min and the minimum 5.13min. Average song bout (period of singing between surfacings) was 11.10min  $\pm$  2.48SD. Song bouts often contained more than one song cycle,

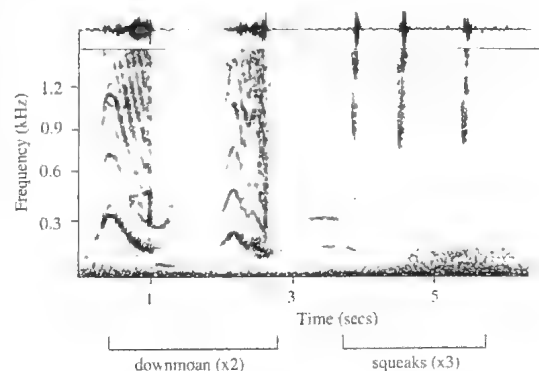


FIG. 4. Sonagram of phrase structure of theme E, a transition theme containing two sound types: 'downsweep' and 'squeaks'. Sampling rate = 5.5kHz, FFT = 1024 pts.

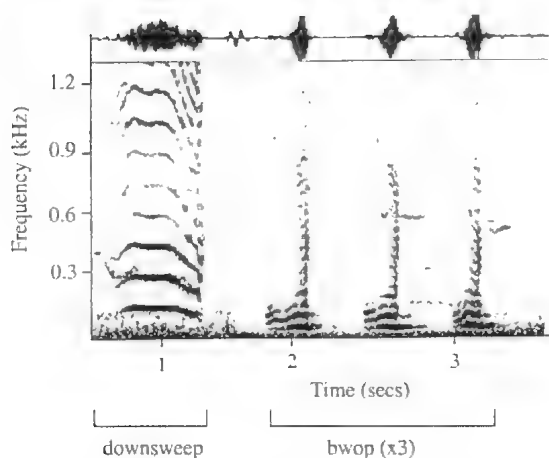


FIG. 5. Sonogram of phrase structure of theme C, comprising two sound types: 'downsweep' and 'bwop'. Number of 'bwops' increased progressively from 1 to 3 as the theme continued. Sampling rate = 5.5kHz, FFT = 1024 pts.

although never more than three. If greater than one song was sung during a song bout, theme A was often omitted and individuals would begin the second song with theme B. This was not a consistent feature either within or between individuals, however it suggests that theme A is a link between song bouts rather than a link between songs cycles. The first song of a song bout was longer (mean 7.366min  $\pm$  1.609SD) than the second song (mean 5.320min  $\pm$  1.576SD).

One aberrant song was identified. Individual 807201 omitted theme B from all songs. The mean song duration was 5.27min ( $\pm$  1.43SD; n = 9).

**MULTIVARIATE AND UNIVARIATE ANALYSIS.** The two sound types used for the analysis of acoustical characteristics are the 'modulated bellow' from theme B and the 'downsweep' from theme C. Theme A could not be used as most individuals surfaced during this theme and the resulting attenuation prevented accurate measurements. Theme E was a transitional theme and contained sound types from the preceding and following themes, B and C respectively.

*Sound Type 1 - Modulated bellow (Mb).* Eight sound units were measured from each of 9 songs for each of the 6

individuals (n = 72). Individual 807201 was not included in the quantitative analysis as theme B did not occur in any of the songs recorded. A MANOVA on the  $\log_{10}$  transformed data showed a highly significant difference between individuals (Wilks' Lambda = 0.242; df 45, n = 72; 1872; p < 0.01). Non-parametric univariate tests demonstrated a highly significant difference between individuals for each of the 9 variables (Table 3).

Box and whisker plots ( $\pm 1.96$ SE) for each variable were created from the multivariate tests to identify variation between individuals. Only three plots have been reproduced here (Fig. 7A-C). There were significant differences between some individuals for one variable and very little variation between the same individual for another variable, with no individual consistently different from the rest.

Although there were significant differences between individuals the variation in the frequency of any frequency variable between individuals is small. For example, the variation in the frequency ( $1.96 \times$  standard error) of the start point (Fig. 7C) for an individual is <0.07 on the logarithmic scale, i.e. about 4%, which corresponds to a difference of <1 semitone. Four individuals show only 1.1% difference in the mean of the start frequency (Fig. 7C). Total variation across all whales was <12% which corresponds to a change in frequency of 2 semitones. The greatest variation in frequency range between individuals is for the ratio of frequencies between inflexion points 1 and 2 at about 23%, less than 4 semitones (Fig. 7B).

*Sound Type 2: Downsweep (Ds).* Three sound units from 9 songs for each of the 6 individuals

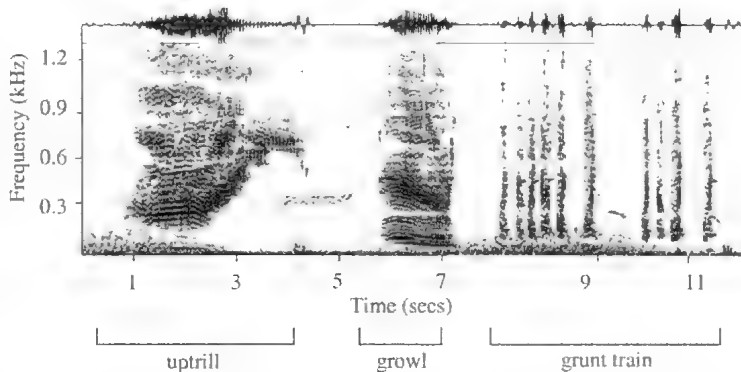


FIG. 6. Sonogram of phrase structure of theme D, comprising three sound types: 'uptrill', 'growl' and 'grunt train'. 'Grunt train' was not present in all repetitions. Sampling rate = 5.5kHz, FFT = 1024 pts.

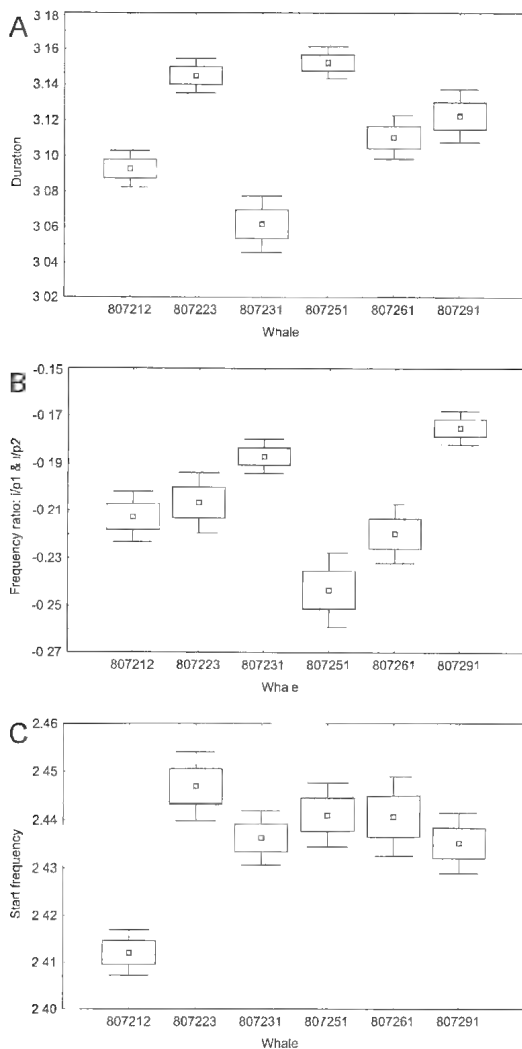


FIG. 7. Box & whisker plots for sound type 1 (modulated bellow) for each whale for the variables: A, 'duration'; B, 'frequency ratio between i/p1 and i/p2'; C, 'start frequency'. Mean,  $\pm 1\text{SE}$  (box) and  $\pm 1.96\text{SE}$  (bar). All values are  $\log_{10}$  transformed.

were included in the analysis ( $n = 27$ ). The MANOVA showed significant differences between individuals (Wilks' Lambda = 0.081; df (35,633);  $p < 0.01$ ). The Kruskal-Wallis ANOVA by Ranks run on each variable independently shows significant differences between individuals for all variables except end frequency (Table 4). Box & Whisker plots ( $\pm 1.96\text{SE}$ ) derived from the MANOVA show the variation between individuals for three variables (Fig. 8A-C).

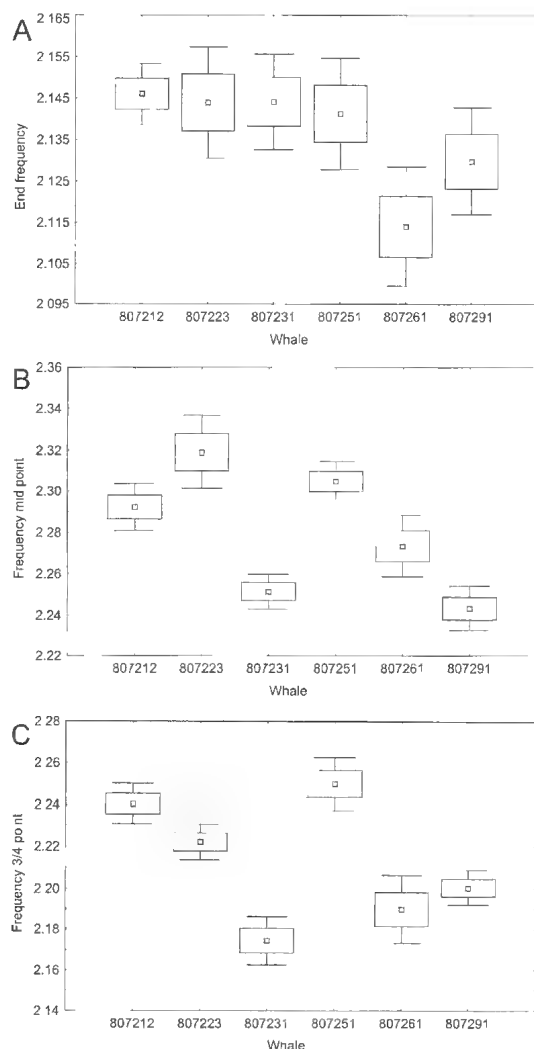


FIG. 8. Box & whisker plots for sound type 2 (downsweep) for each whale for the variables: A, 'end frequency'; B, 'frequency at midpoint'; C, 'frequency at  $\frac{3}{4}$  point'. Mean,  $\pm 1\text{SE}$  (box) and  $\pm 1.96\text{SE}$  (bar). All values are  $\log_{10}$  transformed.

Variation between individuals for each variable is similar for sound type 2 as was found for sound type 1. Although there are significant differences between individuals for each variable the difference between individuals with respect to frequency changes is very low. The greatest difference in frequency values between individuals was 4 semitones. End frequency showed a frequency range of only 2 semitones which corresponds to a 12% change (Fig. 8A).

TABLE 3. Results of Kruskal-Wallis ANOVA for each variable tested independently. df (5);  $p < 0.01$ . All variables were  $\log_{10}$  transformed. Sound type = modulated bellow.

Variable	Chi-sqr	p-level
Start frequency	41.425	$p < 0.001$
End frequency	50.613	$p < 0.001$
Frequency range	67.423	$p < 0.001$
Duration	63.048	$p < 0.001$
No. of inflection pts	49.018	$p < 0.001$
Freq ratio start - i/p1	42.588	$p < 0.001$
Freq ratio i/p1 - i/p2	89.556	$p < 0.001$
Time diff. start - i/p1	50.817	$p < 0.001$
Time diff. i/p1 - i/p2	25.750	$p < 0.001$

CANONICAL DISCRIMINANT FUNCTION ANALYSIS. *Sound Type 1: modulated bellow.* A discriminant function analysis for multiple groups was carried out on the same nine variables. All variables were retained in the model and there was a highly significant level of discrimination between individuals; Wilks' Lambda = 0.241;  $F(45, 1872) = 15.585$ ;  $p < 0.01$ .

The canonical discriminant analysis (CDA) extracted five canonical roots (variables) from the data (number of groups minus 1). Chi-squared tests with successive roots removed indicated that the first four canonical roots resulted in a significant discrimination between groups ( $p < 0.01$ ). However, the first 2 canonical roots accounted for 82% of the discrimination in the data set and so the remaining roots will not be discussed further. The contribution of the original variables to the first 2 canonical roots are shown in Table 5, expressed as standardised  $\beta$  coefficients. The  $\beta$  coefficient measures the respective variables contribution to the discrimination.

The first canonical root (CAN1) was dominated by the variables, frequency ratio start to i/p1 (-1.499) and start frequency (-1.430) both negatively loaded (Table 5). The variable, time difference between i/p1 and i/p2 contributed the least (0.050). The contribution to Root 2 is dominated by the variables frequency ratio between start and i/p1 and frequency ratio between i/p1 and i/p2, both positively weighted with values of 1.524 and 1.339 respectively (Table 5).

The factor structure matrix indicates the simple correlations between the variables and canonical roots. The first canonical root (CAN1) is dominated by duration (-0.582) and number of inflection points (-0.539) both are negatively

TABLE 4. Results of Kruskal-Wallis ANOVA for each variable. df (5);  $N=162$ ;  $p < 0.05$ . Sound type = downsweep.

Variable	Chi-sqr	p-level
Start frequency	28.253	$p < 0.001$
Freq ¼ point	23.370	$p < 0.001$
Freq midpoint	64.070	$p < 0.001$
Freq ¾ point	39.044	$p < 0.001$
End frequency	11.760	$p = 0.038$
Frequency range	23.249	$p < 0.001$
Duration	74.296	$p < 0.001$

weighted (Table 6). CAN2 is dominated by the variables time difference between start and i/p1 (-0.519) and frequency ratio between i/p1 and i/p2 (-0.502). The variable with the least amount of correlation is start frequency (0.043) (Table 6).

A two dimensional plot of the canonical scores for the modulated bellow using the factor matrix (Fig. 9) shows one individual's position relative to another. There is a high degree of overlap which indicates poor discrimination between individuals and no discrete clustering of individuals which would be expected if signature information was present (Fig. 9).

*Sound Type2: downsweep.* The discriminant function analysis showed a significant difference between individuals for six of the seven variables (Wilks Lambda = 0.0813;  $F(35, 633) = 14.76948$ ;  $p < 0.001$ ). Variable frequency range was not significantly different between individuals ( $p = 0.427$ ).

The canonical discriminant analysis (CDA) extracted five canonical roots (variables) with the first four resulting in significant discrimination between groups ( $p < 0.01$ ).

TABLE 5. Standardised  $\beta$  coefficients and Eigenvalue cumulative proportion for the first two canonical roots. All variables  $\log_{10}$  transformed. Sound type = modulated bellow.

Variable	Root 1	Root 2
Start frequency	-1.430	0.587
End frequency	0.065	0.220
Frequency range	-0.391	-0.593
Duration	-0.447	-0.186
No. of inflection pts	-0.251	0.039
Freq ratio start - i/p1	-1.499	1.524
Freq ratio i/p1 - i/p2	-0.945	1.339
Time diff start - i/p1	-0.123	0.516
Time diff i/p1 - i/p2	0.050	0.405
Eigenvalues	0.9305	0.5763
Cumulative proportion	0.5054	0.8184



TABLE 6. Factor structure matrix showing (pooled within-groups correlations) or (correlation variables) for canonical roots 1 and 2. All variables  $\log_{10}$  transformed. Sound type = modulated bellow.

Variable	CAN1	CAN2
Start frequency	-0.279	0.043
End frequency	-0.156	0.144
Frequency range	-0.238	-0.432
Duration	-0.582	-0.069
No. of inflection pts	-0.539	-0.335
Freq ratio start i/p1	-0.193	-0.199
Freq ratio i/p1 i/p2	0.183	0.502
Time diff start - i/p1	-0.018	0.519
Time diff i/p1 - i/p2	0.070	0.127

The cumulative Eigenvalue showed 84% discrimination within the first two canonical roots (Table 7). The standardised  $\beta$  coefficients show duration provided the greatest contribution (0.91) followed to a much lesser extent by frequency range (0.37) (Table 7). CAN2 is dominated by the variable frequency at  $\frac{3}{4}$  point (0.83) with duration contributing little to the discrimination (-0.096) (Table 7).

The factor structure matrix identifies duration as providing the greatest loading to CAN1 (0.806) with a lesser weighting by the variable frequency at midpoint (0.401) (Table 8). CAN2 is primarily weighted by frequency at  $\frac{3}{4}$  point and is positively loaded, (0.829) with a lesser positive loading by the variable frequency at midpoint (0.513) (Table 8).

Canonical scores for CAN1 and CAN2 using the factor matrix correlations for the downsweep are plotted in Fig. 10. There is a level of discrimination between individuals 807223 and 807291 according to CAN1 (x-axis) which is dominated by duration. However, if individual-specific information is present, each cluster would be discrete for each individual. There is considerable overlap between individuals 807212 and 807251 (Fig.10), however it is unlikely they are the same individual as the recordings were separated by a period of 4 days. Further, they are well separated in Fig. 9.

## DISCUSSION

**SONG PATTERN AND STRUCTURE.** The song pattern of the east Australian population of humpback whales during the northward migration in 1998 conforms to the structural 'rules' first described for populations in the

TABLE 7. Standardised  $\beta$  coefficients showing the contribution of each variable to the first two canonical roots. All variables  $\log_{10}$  transformed. Sound type = downsweep.

Variable	CAN1	CAN2
Start frequency	0.264	-0.468
Freq at $\frac{1}{4}$ point	-0.125	0.228
Freq midpoint	0.247	0.524
Freq at $\frac{3}{4}$ point	0.029	0.834
End frequency	0.311	-0.542
Frequency range	0.372	-0.354
Duration	0.914	-0.096
Eigenvalue	2.349	1.133
Cumulative proportion	0.569	0.844

northern hemisphere (Payne & McVay, 1971; Payne, 1983) and is similar to those described for this population (Cato, 1991). The song is well structured and comprises nine sound types which combine to form five themes. These themes occur in a fixed order and are a powerful constraint on the pattern of the song. Frequency range of all sound types was 50Hz-6000Hz and is similar to the frequency ranges published for the east Australian population (Mednis, 1991). Mean song duration was 7.99 minutes  $\pm$  2.61SD (n = 115). This is less than that described by Cato (1991) for the 1982-1983 song (for the same population), which had a mean duration of 9.25min. Variation in song duration between years is most likely a result of the difference in the number of sound types and themes.

**DISCRIMINATION BETWEEN INDIVIDUAL SINGERS.** Both multivariate and univariate tests showed significant measurable differences between individuals for all parameters included in the analysis. However, there was no observable pattern and no consistent differences between individuals. If differences in song pattern and structure are to be useful, differences would be

TABLE 8. Factor structure matrix for CAN1 and CAN2. All variables  $\log_{10}$  transformed. Sound type = downsweep.

Variable	CAN1	CAN2
Start frequency	0.304	-0.162
Freq at $\frac{1}{4}$ point	0.295	0.084
Freq midpoint	0.401	0.513
Freq at $\frac{3}{4}$ point	0.069	0.829
End frequency	0.010	0.133
Frequency range	0.309	-0.009
Duration	0.806	-0.149

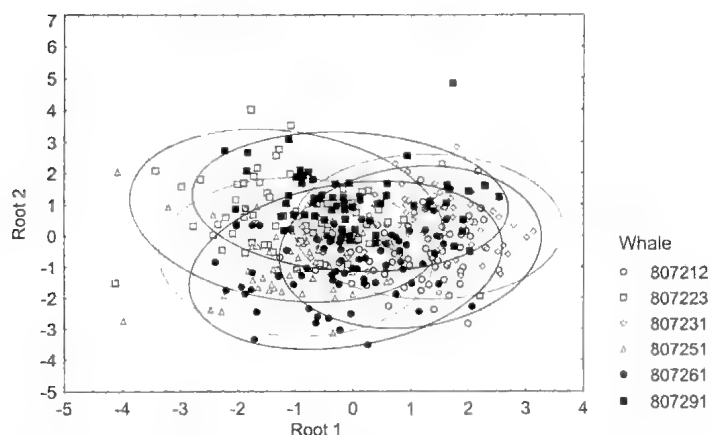


FIG. 9. Scatterplot of canonical scores for sound type 1 (modulated bellow). CAN 1 & CAN 2 accounted for 82% of discrimination. CAN 1 is dominated by the variables 'duration' and 'number of inflection points', both negatively weighted. CAN 2 is dominated by the variables 'time difference between start and i/p1' and 'frequency ratio between i/p1 and i/p2', both negatively weighted. Total variables in the model = 9.

expected to occur between all individuals for a particular variable.

The frequency range within each sound type shows that individuals consistently produce sounds which vary by <12% (2 semi-tones) and the variation in frequencies between individuals was ~23% (<4 semi-tones). The precision with which individuals produce each sound type suggests that humpback whales have a well-refined perception of frequency. Therefore, even small changes (~3 semi-tones) should be sufficient for an individual to be distinctive. Given the complexity of the song, the extensive time allocated to song production and the perceived importance of song in the reproductive cycle of humpback whales, producing consistent sounds may be important. The changes described in humpback whale song over time are cultural, in that they are due to learning of a vocal behavioural pattern (Payne & Payne, 1985; Cato, 1991). Noad et al. (2000) reported a rapid change in song over successive seasons and, terming it 'cultural revolution', suggested that novelty drives change. The apparent precision with which the humpback whales in this study produced sounds would facilitate

this rapid change. However the rapid replacement of song would tend to work against development of individual differences.

Results of the canonical analysis demonstrated that most discrimination between individuals could be explained by duration, for both sound types analysed. Longer call duration has been demonstrated to be more attractive to female grey tree frogs (Gerhardt, 1991) and Pacific tree frogs (Whitney & Krebs, 1975). However, clusters are weak and there is considerable overlap between clusters suggesting poor discrimination between individuals. Increased signal duration has been related to increased energetic output in anurans and increased energetic cost of a signal appears to be a

feature generally attractive to females in male display calls (Taigen & Wells, 1984). Helweg et al. (1992) suggested that song production in humpback whales may represent a relatively small portion of the energy budget and suggested it is unlikely that females use duration as a measure of energetic output.

Stereotype of humpback whale song is one characteristic which has been stressed in the literature. Complexity, however, can be seen in the ways that singers vary the songs they produce

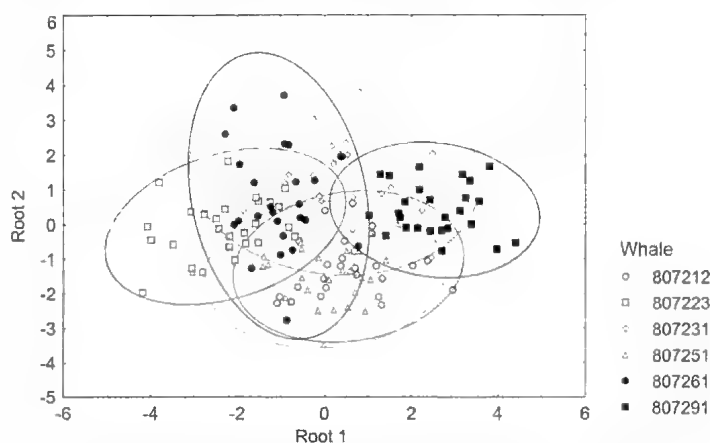


FIG. 10. Scatterplot of canonical scores for sound type 2 (downsweep). CAN 1 & CAN 2 accounted for 84% of discrimination. CAN 1 is dominated by the variables 'duration' and 'frequency at midpoint', both positively weighted. CAN 2 is dominated by the variables 'frequency at 3/4 point' and 'frequency at midpoint', both positively weighted. Total variables in the model = 7.

within a single session, for example in terms of how many times each phrase is repeated. Within-population studies among European warblers and other species has revealed a relationship between repertoire size and components of fitness. European warblers with larger repertoire sizes may pair earlier (Catchpole, 1983) or obtain more mates (Catchpole, 1986). Yasukawa et al. (1980) found a correlation between repertoire size and harem size in red-winged blackbirds.

If repertoire size could be paralleled with song complexity in humpback whales then perhaps the functional unit of humpback whale song is the pattern and degree of complexity within phrases and themes rather than the acoustical characteristics of the component parts. Tyack (1981) argued that song complexity is the result of inter-sexual selection. This implies that active female choice has occurred. Theories of sexual selection based on female choice rely upon the assumption that females actively choose their mates, rather than just experiencing passive attraction to the nearest male stimulus. Active choice must involve sampling several males and rejecting some before a choice is made. Dale et al. (1990, 1992) demonstrated that female pied flycatchers visit up to nine singing males before selecting a mate. Female great reed warblers take up to three days to select a mate and during this time will visit, on average, six male territories before making a selection (Bensch & Hasselquist, 1992).

For humpback whales, Helweg et al. (1992) proposed that singers maintain a 'spatially dynamic array through which females pass'. Females can then listen to singers and select a mate based on some characteristic within the song. Tyack (1981) found that singers frequently joined, or were joined by, other whales which resulted in the cessation of singing. Further, some of the whales which joined singers were determined to be females lending support to the theory that singing serves to attract females (Tyack, 1981; Medrano, et al., 1994).

However, females may not actively choose males; 'selection' may closer reflect passive choice, whereby females exercise choice by allowing potential mates to join her (Helweg et al., 1992; Frankel, 1994). Results from playback experiments have shown that few whales approach the playback of song (Tyack, 1983; Mobley et al., 1988). The most 'attractive' vocalisations are feeding calls or social sounds, which are indicative of a female being present. During

both summer and winter the social structure of humpback whales is fluid with many small groups associated for brief periods. However, larger groups are often seen during the winter migration. In these larger groups substantial surface activity occurs, ranging from low level 'passive' behaviours to direct physical contact between members. These 'competitive' groups consist of multiple mature males competing for sexual access to a single mature female (Tyack & Whitehead, 1983; Baker & Herman, 1984; Clapham, et al., 1992). Females then select mates based on outcomes of these competitive associations. Therefore, song may function to advertise location to both males and females, but it may be the results of direct competitive behaviour between males that influences female choice.

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### GEOGRAPHICAL AND TEMPORAL MOVEMENTS OF HUMPBACK WHALES IN WESTERN AUSTRALIAN WATERS. (ABSTRACT)

This report was initiated by a research grant from Woodside Energy to interpret the timing of movements of humpback whales (*Megaptera novaeangliae*) through the Kimberley region of north Western Australia. Through extra funding by Environment Australia, the scale of the project was expanded to an analysis of the Western Australian photo-identification catalogue for the purpose of describing the temporal and spatial movements of these whales, as completely as possible, along their entire migratory route. Through compilation of historical whaling data, recent aerial and boat-based survey data, a general framework for the overall peaks of migration has been estimated. Data to be obtained from the analysis of individually identified whales using a computerised matching system is expected to add further detail and accuracy to these estimates at the completion of this project (May 2001).

The migratory paths of humpback whales along the Western Australian coast can be expected to lie within the continental shelf boundary or 200m bathymetry. Major resting areas along the migratory path have been identified at Exmouth Gulf (southern migration only) and at Shark Bay.

The northern endpoint of migration and resting area for reproductively active whales in the population appears to be Camden Sound in the Kimberley. A 6,750 square mile area of the Kimberley region, inclusive of Camden Sound, has also been identified as a major calving ground. The northern and southern migratory paths have been shown to be divergent at the Perth Basin, Dampier Archipelago and Kimberley regions. In all cases the northern migratory route is further off-shore.

Data from photographically resighted individuals suggests that singers (reproductively active male whales) may have the slowest migratory rate of all measured age and sex classes in the population, including cow/calf pods. However, current migratory rate estimates, when compared with historical whaling data, are likely to be negatively biased since they are measured across regions that include resting areas. Estimates of residency periods in resting areas gained from photographic resight analysis can be expected to help quantify this bias.

Curt & Micheline-Nicole Jenner and K. McCabe, Centre for Whale Research (WA) Inc., PO Box 1622, Fremantle 6959, Australia; 29 August 2000.

### REAL TIME TRACKING OF HUMPBACK WHALES. (ABSTRACT)

For several years a team of researchers has been based at Byron Bay for a two-week period to observe, photograph and identify humpback whales (*Megaptera novaeangliae*). In the past, compass binoculars and a crude device called a TCM card were used to obtain a pod's position. Optical theodolites were later used to acquire more accurate locations of whale pods but required large amounts of post processing. Since 1998 staff and students from the University of Newcastle have assisted in the Cape Byron Whale Research Project by using their surveying skills to measure pod locations. A real time tracking system called 'Cyclops' has been developed. The system consists of a theodolite or total station connected to a personal computer (Windows 95/NT). Once the instrument is pointed to a pod, the horizontal and vertical angles are directly sent to the computer. 'Cyclops' then calculates the position of the pod

correcting for tides, earth curvature and refraction. The program determines which pod was observed and plots its position on a map shown on the computer screen, as well as the pod's makeup, activity, speed, course, distance, direction and time of observation. The program also allows for factors such as weather conditions and visibility to be input as well as having the capability of predicting a pod's position at any time based on its average speed and course. The system has helped in obtaining accurate position fixes of whale pods in real time and displaying the information in a useful manner.

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### AUSTRALIAN WHALE-WATCH REGULATIONS AND GUIDELINES: ARE OPERATORS COMPLYING? (ABSTRACT)

Effective management of the whale-watch industry is dependent on operators' compliance with the appropriate management regimes. Operators' compliance with existing regulations and guidelines and the manner in which regulations have been enforced have not been studied in detail. Different management and regulatory strategies across adjacent jurisdictions are present in Australia, thus allowing for their comparison.

The study aims to test whether existing distance and approach conditions for whale-watch vessels are an effective regulatory tool. Although National Guidelines have been introduced in Australia, regulatory controls differ between states, allowing a comparison of management strategies. A combination of observational data and qualitative surveys are being used to elicit the full picture of the effectiveness of these strategies. Movements of whale-watch vessels in relation to

focal humpback whale pods in Queensland and New South Wales were plotted. This provided an indication of operators' compliance with distance and approach guidelines and regulations. Questionnaire surveys were used to elicit the potential influence of operators' beliefs and perceptions concerning the whale-watch guidelines on compliance.

Results to date are indicative of a high level of compliance to the whale-watch guidelines/regulations. Almost all instances of vessels in closer proximity than 100m to the whales were due to the movement of the pod towards the vessel. Additionally, survey questionnaire data reflect approval of the regulations/ guidelines, thus supporting the quantitative result.

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# CHARACTERISTICS OF THE NEW CALEDONIAN HUMPBACK WHALE POPULATION

CLAIRE GARRIGUE, JACQUI GREAVES AND MAGALY CHAMBELLANT

Garrigue, C., Greaves, J. & Chambellant, M. 2001 12 31: Characteristics of the New Caledonian humpback whale population. *Memoirs of the Queensland Museum* 47(2): 539-546. Brisbane. ISSN 0079-8835.

Data collected from 1995 to 2000 in the lagoon of New Caledonia show that between June and November this area is used as a breeding and calving ground for humpback whales, with peak abundance in August. Analyses of photo-identification data and acoustic recordings suggest that this population is a component of the Area V stock. To date, 206 humpback whales have been individually identified. Photo-ID comparisons prove migratory movements between New Caledonia and each of eastern Australia, New Zealand and Tonga. The constant increase in re-sightings of individuals from 1996 to 1998 suggests that the population is not large with an estimate of 314 ( $\pm 72$ ) using a weighted mean of the Petersen estimate. Crude birth rate was calculated at 3.4-10% per year. The most commonly encountered pod types were singles (39%) and pairs (31%). Occurrences were greater in August and July. Reproductive groups (16%) and cow and calf pairs (11%) were most often observed in August. Size structure of the population was dominated by large whales (83%). A maximum length of stay of 60 days was observed for a male. A sex-ratio of 1.9:1 in favour of males was calculated. Numbers observed in 1999 were low as were reproductive groups.

□ Humpback whale, New Caledonia, population estimate, social structure, migration.

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In New Caledonia the arrival of the humpback whale (*Megaptera novaeangliae*) has long been recorded in the Melanesian calendar, and is an important component of traditions and legends (Garrigue & Greaves, 1999). First documented occurrences of humpback whales in New Caledonian waters come from whaling records of the 19th Century (Townsend, 1935; Pisier, 1975). While some whaling occurred at Lifou and Maré in the Loyalty Islands east of New Caledonia, it appears that it was more concentrated in the Chesterfield Islands in the Coral Sea to the west. Anecdotal reports suggest that humpback whales frequented New Caledonia until at least the 1950's, prior to the collapse of all Southern Hemisphere stocks.

In the course of initial field observations and photographic identification of humpback whales during a five day survey in 1993 and a two week survey in 1994, Gill et al. (1995) observed behaviour associated with reproductive activity. This, in addition to the presence of mother and calf pairs, suggested that New Caledonia is a reproductive area for this species (Garrigue & Gill, 1994). This preliminary research identified New Caledonia as a winter migratory destination for Area V humpback whales.

To improve knowledge of this population, surveys of two months duration were conducted

annually from 1995 and those results are presented in this paper.

## METHODS

**STUDY AREA.** New Caledonia is part of Melanesia, situated in the southwest Pacific Ocean just north of the Tropic of Capricorn, east of Australia and northwest of New Zealand (Fig. 1). It occupies 1,450,000km<sup>2</sup> lying between 18°-23°S and 158°-172°E. Grande Terre, the main island of the archipelago, is 400km long and 50-80km wide. It is surrounded by over 1,600km of barrier reef that delineates a lagoon of 24,000km<sup>2</sup> with a mean depth of 24m. Two groups of small islands are inside this lagoon, the Belep Islands to the north, and the Isle of Pines to the south. Outside the lagoon to the east are the Loyalty Islands: Maré, Lifou and Ouvea. This study was conducted in the southern part of the lagoon, off the main island of Grande Terre.

**STUDY PERIODS AND SURVEY METHODS.** Since 1991, forms have been distributed to professional and recreational boat users throughout New Caledonia to obtain general information on observations of marine mammals (Garrigue & Greaves, 2001).

Since 1995 we conducted two- to three-month field surveys between July and September in the



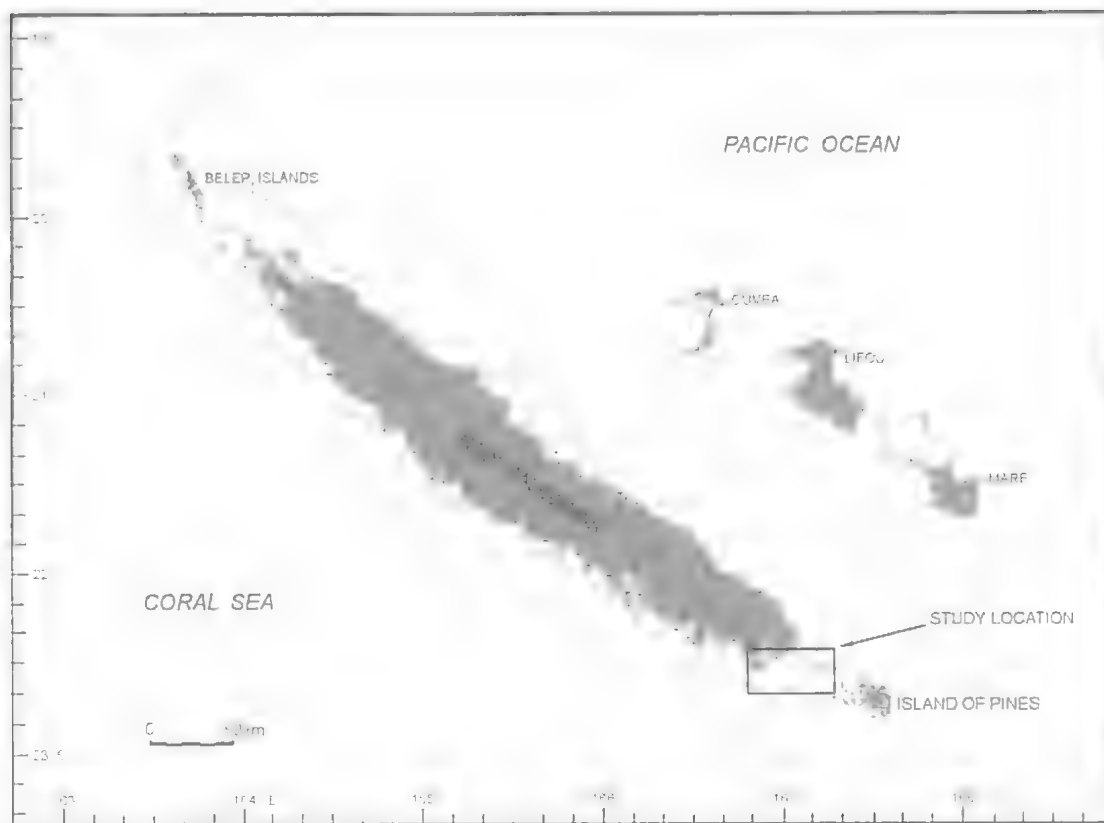


FIG. 1. Islands of New Caledonia, and study region.

southern lagoon between 22°20'–22°40'S, and 166°50'–167°07'E, covering approximately 1,000km<sup>2</sup>.

During these dedicated surveys, a land-based team searched for whales from an elevated point (189m) using hand-held binoculars (7 × 42mm) and a telescope. Position and behaviour of pods were recorded and transmitted via VHF radio to a research vessel. Boat-based observations were carried out mainly from a 6m semi-rigid inflatable equipped with two 40hp outboard motors.

Surveys were conducted on all days, weather conditions permitting (wind <20 knots and no rain). There was no *a priori* selection of whale groups of a specific size or composition.

For each observed pod, the time, location (GPS position), group size, pod composition and behaviour were noted. Pod composition included: single, pair, mother and calf, mother-calf and escort, and competitive group, following the definitions of Tyack & Whitehead (1983), Baker & Herman (1984) and Clapham et al. (1992). Data were recorded on micro-cassette recorders,

and transcribed each night onto data forms for later database entry.

Individual humpback whales were photographed as often as possible for identification through unique markings on the ventral surface of the tail flukes (Katona et al., 1979). SLR cameras equipped with 200 and 300mm lenses and 100 or 400ASA slide film were used for photo-identification.

Tissue samples were collected using a cross-bow and specially adapted bolt (Lambertsen et al., 1994.). Skin was placed in ethanol and fat was wrapped in pre-heated (550°C) aluminium foil. Samples were then deep frozen for later analyses. Humpback whale songs were recorded using a hydrophone with preamplifiers and an analogue cassette tape recorder (Sony WM-D6C).

#### DATA ANALYSIS

Whale occurrence, the composition of pods and size of individuals were recorded. Gender was identified by amplification of the male specific gene SRY (Gilson & Syvanen, 1998).

TABLE 1. Sampling effort and number of humpback whales sighted from sea- and land-based surveys.

Year	Month	Study effort					Sightings			
		Sea-based			Land-based		Sea-based		Land-based	
		Days of effort	Hrs of observation	Nautical miles	Days of effort	Hrs of observation	Number of pods	No. of whales	No. of pods	No. of whales
1995	July	3	10:45	90	1	2:00	4	7	4	7
	August	14	63:45	484	12	40:35	16	34	24	34
	September	15	72:35	482	19	85:57	6	18	19	36
	<b>Total</b>	<b>32</b>	<b>147:05</b>	<b>1056</b>	<b>32</b>	<b>128:32</b>	<b>26</b>	<b>59</b>	<b>47</b>	<b>77</b>
1996	July	16	105:34	687	15	75:12	22	50	29	43
	August	27	195:27	1223	27	139:09	39	68	67	103
	September	13	79:46	651	10	63:22	3	9	8	15
	<b>Total</b>	<b>56</b>	<b>380:47</b>	<b>2561</b>	<b>52</b>	<b>277:43</b>	<b>64</b>	<b>127</b>	<b>104</b>	<b>161</b>
1997	July	15	93:30	333	14	67:08	25	47	32	46
	August	27	192:53	1325	27	146:47	27	57	33	51
	September	1	6:19	50	1	4:50	2	4	2	3
	<b>Total</b>	<b>43</b>	<b>292:42</b>	<b>1708</b>	<b>42</b>	<b>218:45</b>	<b>54</b>	<b>108</b>	<b>67</b>	<b>100</b>
1998	July	25	162:30	1280	27	115:27	11	27	13	25
	August	16	114:01	857	14	71:41	19	43	26	48
	September	9	63:35	549	10	47:04	10	19	16	27
	<b>Total</b>	<b>50</b>	<b>340:06</b>	<b>2687</b>	<b>51</b>	<b>234:12</b>	<b>40</b>	<b>89</b>	<b>55</b>	<b>100</b>
1999	July	22	139:02	1186	22	100:09	10	16	9	13
	August	23	169:03	1341	21	122:29	18	34	19	29
	September	1	4:00	54	0	0	0	0	0	0
	<b>Total</b>	<b>46</b>	<b>308:05</b>	<b>2581</b>	<b>43</b>	<b>222:38</b>	<b>28</b>	<b>50</b>	<b>28</b>	<b>42</b>
2000	July	17	123:45	926	16	73:34	16	26	10	17
	August	23	157:53	1190	18	94:08	24	49	21	36
	September	10	74:43	545	8	47:40	13	28	11	21
	<b>Total</b>	<b>50</b>	<b>356:21</b>	<b>2661</b>	<b>42</b>	<b>215:22</b>	<b>53</b>	<b>103</b>	<b>42</b>	<b>74</b>
<b>TOTAL</b>		<b>277</b>	<b>1825:06</b>	<b>13254</b>	<b>262</b>	<b>1297:12</b>	<b>265</b>	<b>536</b>	<b>343</b>	<b>554</b>

Population abundance was estimated across the six year study using mark-recapture photographic methodology allowing individual distinctiveness (see Friday et al., 2000) and the weighted mean of the Petersen estimate (Seber, 1982). Crude birth rates were calculated following Clapham & Mayo (1990).

Movements of humpback whales in the South Pacific area were established by comparing those identified in New Caledonia, until 1999, with those in published catalogues from east Australia ( $n = 1,088$ ) (Kaufman et al., 1993), Tonga ( $n = 247$ ) (Patenaude & Baker, 1996; unpubl. data) and New Zealand ( $n = 4$ ) (Patenaude & Baker, 1996; unpubl. data) (Garrigue et al., 2000b). During a workshop held at the University of Auckland in March, 2000 (Donoghue & Baker, 2000) New Caledonian sightings were also compared with those identified in French Polynesia ( $n = 138$ ) (Poole, unpubl. data), the

Cook Islands ( $n = 23$ ) (Hauser & Peckham, unpubl. data), Colombia ( $n = 20$ ) (Fundacion Yubarta, unpubl. data), Ecuador ( $n = 59$ ) (Instituto Antartico Chileno, unpubl. data) and the Antarctic Peninsula ( $n = 23$ ) (Instituto Antartico Chileno, unpubl. data).

## RESULTS

### SAMPLING AND DATA COLLECTION.

*Sampling Effort.* During the last six survey years a total of 277 days representing >1,800 hours were spent at sea and 262 days representing ~1,300 hours spent at the land observation point (Table 1).

A comparison of the number of pods seen by the land- and sea-based teams is shown in Fig. 2. Until 1998 more pods were observed from land than from sea but this pattern was reversed in 2000.

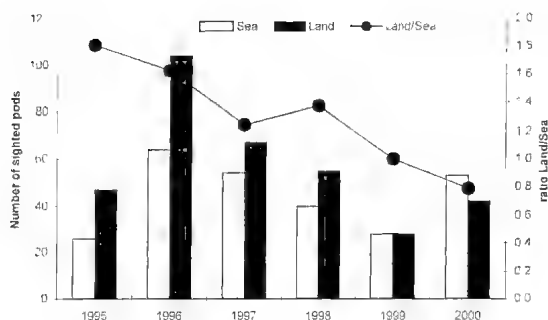


FIG. 2. Number of pods observed from land and sea.

**Datasets and Collection.** From >800 photographs 206 humpback whales were identified from the ventral surface of the flukes alone, or combined with dorsal fin/lateral body markings ( $n = 202$ ), or by lateral body markings with dorsal fin alone ( $n = 4$ ) (Garrigue & Greaves, 1999).

Two hundred and seventeen skin samples and 197 blubber samples were collected during the six-year study and are presently being analysed.

Songs were recorded since 1992 with ~60 recordings available for analysis. Some acoustic comparisons have been completed (Gill et al., 1995; Helweg et al., 1998; Helweg et al., 2000); others are in progress.

**OCCURRENCE.** Of the 466 marine mammal observation forms returned in the 9 years from 1991-1999, 269 included humpback whales, with sightings from all around New Caledonia. Earliest sightings predominated in June and the latest in December, although occasional sightings were recorded at other times (Fig. 3). Eighty per cent of reported observations were made in the winter (July, August and September) (Fig. 3). Data from the dedicated surveys of 1995-1999 show the peak of season was always in August, when >50% were observed (Fig. 3).

During land-based surveys, 343 pods comprising 554 whales were sighted. At sea, 265 pods comprising 536 whales were encountered over the six years. Monthly observations are summarised in Table 1. It should be noted that numbers decreased from 1996 until 1999 and that 1999 was particularly low (Fig. 4). The July 1995 survey was atypical, being 30 days later than for subsequent years.

**POD OCCURRENCE, COMPOSITION, SIZE AND SIZE STRUCTURE.** Social composition was recorded for 253 of the 265 pods sighted (Table 2). Over the six year survey the most commonly observed pod types were singles (39%)

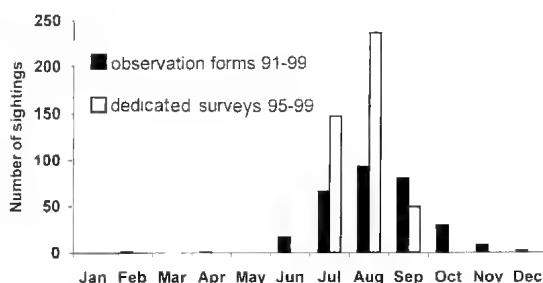


FIG. 3. Monthly observations of humpback whales.

and pairs (31%). Reproductive groups comprised 16% and mother-calf pairs 11%. Least represented groups were mother-calf and escort groups, and mother and calf in reproductive groups, comprising only 2% of encountered pods.

Mean pod size was 2.02.

Social composition of pods varied intra-seasonally (Fig. 5). In July, singles and pairs were more frequent; in August these were less frequent but mother-calf groups increased. In September this pattern was repeated along with an increase of reproductive groups including cows and calves; mother-calf and escort groups were also more common.

Whale sizes, although difficult to estimate, were classified using: small (for calf), medium (~8m or smaller) and large (>8m) (Table 3). During a season the population structure was dominated by large whales, representing >80%, except in 1999 when large whales were 64%, while medium-sized whales (24%) were seen in greater numbers than during previous years.

**SEX COMPOSITION OF THE POPULATION.** Skin samples were taken from 140 of the 206 identified whales and analysed for gender. Two percent of the samples gave inconclusive results; 65% of the sexed whales were male and 35%

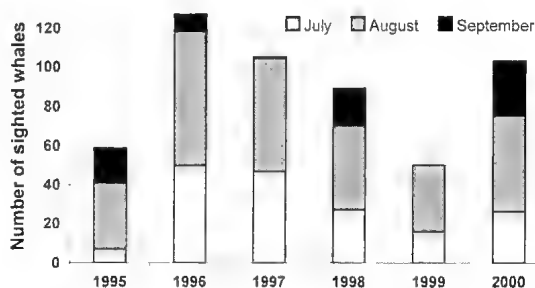


FIG. 4. Monthly observations of humpback whales by year of survey.

TABLE 2. Composition of sighted pods (Sn, single; Pr, pair; MC, mother and calf; MCE, mother, calf and escort; MC in CG, mother and calf in competitive group; CG, competitive group).

Year	Month	Sn	Pr	MC	MCE	MC in CG	CG
1995	July	1	2	0	0	0	1
	Aug	6	5	1	0	1	3
	Sept	1	2	0	1	0	2
	<b>Total</b>	<b>8</b>	<b>9</b>	<b>1</b>	<b>1</b>	<b>1</b>	<b>6</b>
1996	July	11	4	1	0	0	5
	Aug	15	13	5	0	0	3
	Sept	0	0	1	1	1	0
	<b>Total</b>	<b>26</b>	<b>17</b>	<b>7</b>	<b>1</b>	<b>1</b>	<b>8</b>
1997	July	11	9	0	0	0	2
	Aug	7	10	5	0	0	3
	Sept	1	2	0	0	0	0
	<b>Total</b>	<b>19</b>	<b>21</b>	<b>5</b>	<b>0</b>	<b>0</b>	<b>5</b>
1998	July	2	4	1	0	0	2
	Aug	9	3	1	0	0	6
	Sept	4	3	1	0	0	3
	<b>Total</b>	<b>15</b>	<b>10</b>	<b>3</b>	<b>0</b>	<b>0</b>	<b>11</b>
1999	July	4	3	2	0	0	0
	Aug	6	4	3	1	0	3
	Sept	0	0	0	0	0	0
	<b>Total</b>	<b>10</b>	<b>7</b>	<b>5</b>	<b>1</b>	<b>0</b>	<b>3</b>
2000	July	7	5	1	0	0	2
	Aug	9	8	3	0	1	4
	Sept	5	1	2	1	1	2
	<b>Total</b>	<b>21</b>	<b>14</b>	<b>6</b>	<b>1</b>	<b>2</b>	<b>8</b>
<b>TOTAL</b>		<b>99</b>	<b>78</b>	<b>27</b>	<b>4</b>	<b>4</b>	<b>41</b>

female. The sex-ratio was thus 1.9:1 in favour of males.

**ESTIMATION OF ABUNDANCE AND CRUDE BIRTH RATE.** From 1996 to 1998 the year-to-year re-sighting rate increased to >29%; decreasing to 5% in 1999 (Fig. 6). Forty six whales representing 22% of identified animals were re-sighted at least once, of which 50% were identified as males and 26% females. Not only were the same individuals sighted inter-annually, but they were observed several times intra-seasonally.

These observations suggest that the population is small. Using a weighted mean of the Petersen estimate the population was estimated at  $N = 314$  (95% CI: 243-386) (Table 4). Crude birth rate was estimated following Clapham & Mayo (1990), at 3.4-10% (Table 5).

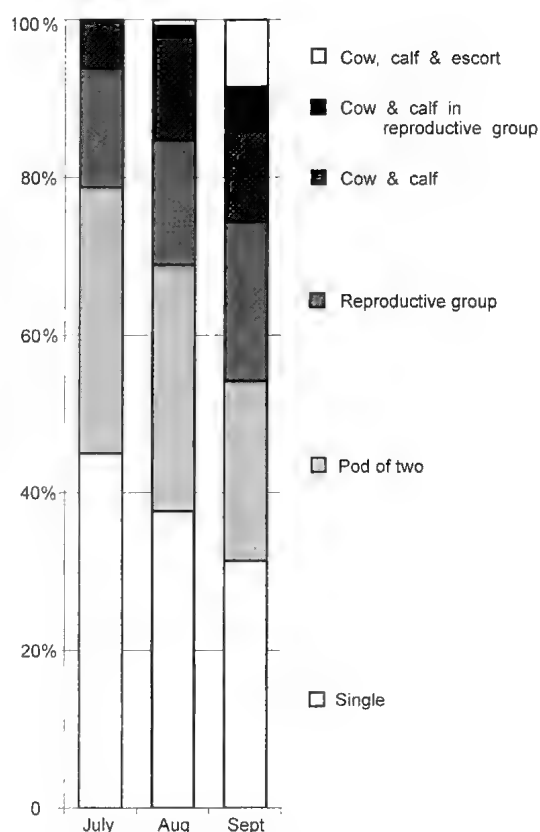


FIG 5. Monthly observations of social pods, 1995-2000.

**INTRA-SEASONAL RESIGHTS.** Fifty-nine whales, ~1/3 of identified individuals, were observed from 2-4 times during a single season. Most resights within a season were males (69% of the sexed whales) and the duration of stay was longer than that of females (average length of stay = 17 days for males and 10 days for females without calf). The maximum length of stay was 60 days by a male (observed on 7 July, 15 August and 5 September, suggesting residency for the

TABLE 3. Size structure of humpback whale sightings.

Year	No. of whales	% Small (calf)	% Medium	% Large
1995	35	8.5	8.5	83
1996	72	11	6	83
1997	72	5.5	14	80.5
1998	63	5	3	92
1999	41	12	24	64
2000	67	8	5	87
<b>TOTAL</b>	<b>283</b>	<b>8</b>	<b>9</b>	<b>83</b>

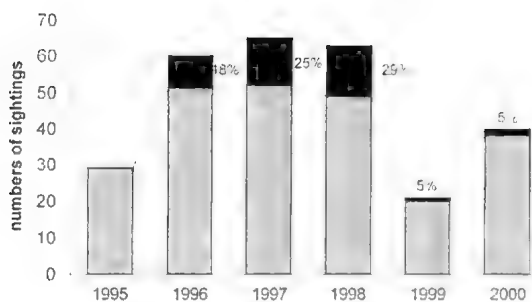


FIG. 6. Re-sighting rates (black).

entire period). The few females observed for a period >1 week were accompanied by calves.

**MIGRATION.** Ten humpback whales were sighted both at New Caledonia and another area of the South Pacific (Garrigue et al., 2000a, b). Seven were in migratory corridors (five in east Australia and two in New Zealand) and three during 1999 in the Tongan breeding grounds.

#### DISCUSSION

Humpback whales are present in New Caledonia during the austral winter. The seasonal peak is in August, earlier than in other more easterly breeding grounds such as Tonga, the Cook Islands and French Polynesia (M. Donoghue & N. Hauser, pers. comm.; Poole, pers. comm.). High numbers of opportunistic observations (marine mammal survey data) in September are probably explained by the occurrence of school holidays, and the usually mild weather conditions which favour recreational boating.

The presence of small, pale and uncoordinated calves, some with folded over dorsal fins, is evidence that the lagoon in the south of New Caledonia is a calving ground. Observation of reproductive groups and the acoustic detection of many singers provides evidence that this is also a mating area. The temporal usage pattern of this breeding ground by different social groups agrees with Chittleborough (1965) who concluded that certain age/sex classes of the population travel ahead of others. Our findings concerning the different length of stay of males and females concur with Matthews (1938) who suggested that mature females leave the breeding ground as soon as they are fertilised. The male-biased sex-ratio of the population has also been described on other breeding grounds (Dawbin & Falla, 1949; Brown et al., 1995).

The Area V stock of humpback whales is described by Dawbin (1966) as the group that

summer in the Antarctic between 130°E-170°W, then migrate past eastern Australia or New Zealand to reach their tropical winter breeding grounds. Photographic comparison of humpback whales seen in New Caledonia with those seen in Australia and New Zealand, and acoustic analyses of recordings from the three regions demonstrate that the population located around New Caledonia is a component of the Area V stock. In question is whether New Caledonia forms an extension of the east Australian group, or should be considered part of the New Zealand group as described by Dawbin (1966). The photo-ID comparison was not helpful in resolving this question, as exchanges were found with eastern Australia (5), New Zealand (2) and Tonga (3). Acoustic analysis demonstrated that east Australia and New Caledonia songs were not significantly different (Helweg et al., 1998). However, the demographic trend (i.e. no evidence of population increase) and the high re-sight rates within New Caledonia suggest a degree of subdivision between these regions. Genetic analyses currently in progress may answer this question.

The increase in inter-annual re-sighting rate from 1996 to 1998 suggests that the local population is not large. This is supported by the population estimate. This estimate must be interpreted with some caution as the Petersen method assumes that the population is closed with no immigration or emigration, yet our data show that there is some exchange between breeding grounds (Garrigue et al., 2000a, b). Equal 'catchability' of individuals in the population is another assumption that is possibly violated, as fluke photographing is largely opportunistic. For example, mothers with small calves seldom perform a fluke-up dive, which renders them temporarily unavailable for sampling. In any case, the estimate indicates that the abundance of humpback whales in New Caledonia is relatively low, numbering only a few hundred. This is in stark contrast to the situation off eastern Australia where the number of humpback whales passing along the coast has increased markedly over the last decade (Brown et al., 1997; Paterson et al. 1994, 2001) with a 1999 estimate of 3,600 individuals.

The smaller percentage of large whales observed in 1999 probably explains the low number of competitive groups that were also observed. This corroborates the weak acoustic detection rate (i.e. singing) in that period. The decrease in the ratio between pods seen from land and from sea needs further investigation. This decrease may be due

TABLE 4. Population estimates.

	1995	1996	1997	1998	1999	2000
Marked whales in current year (ni)	29	51	52	49	20	38
Number of re-captures (mi)	3	11	20	20	6	14
Marked whales from previous years (Mi)	27	53	93	125	154	167
N (estimate)						314

to: an effect of the observers and/or of weather conditions; improved sighting skill of the vessel-based team; a shift of whales further off-shore (possibly related to the unregulated development of whale watching cruises); or other causes. These results, when considered with the inter-annual resighting rate and the increase of crude birth rate in 1999 and 2000, demonstrate a change in the characteristics of the New Caledonian humpback whale population.

Results of the six-year dedicated survey show that the southern part of the New Caledonian lagoon is a breeding ground for humpback whales during the austral winter. It is known that other parts of the large lagoon bounding the main island are also used. Ouvea and isolated atolls, such as the Chesterfield area (~600kmNW of the study site) (cited by Townsend, 1935 as a whaling ground) and Surprise (NW New Caledonia) are also possible breeding grounds. Future research should confirm this. The study of humpback whales in New Caledonia (including collection of photo-ID, skin and blubber samples, song recordings and behavioural data) will continue in order to contribute to a larger survey of humpback whales in the tropical South Pacific (Anonym., 2001). A comparison of genetic samples and photo-ID data collected over a wide area, including eastern Australia, New Zealand, New Caledonia, Tonga, Cook Islands and French Polynesia, will improve knowledge of humpback whales in the South Pacific.

#### ACKNOWLEDGEMENTS

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TABLE 5. Crude birth rate.

Year	Number of Calves (Tc)	Number of sighted whales (Ti)	Tc/Ti %
1995	3	59	5.1
1996	8	127	6.3
1997	4	108	3.7
1998	3	89	3.4
1999	5	50	10.0
2000	9	103	8.7
Mean	5	89	6.0

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## MORTALITY AND ANTHROPOGENIC HARASSMENT OF HUMPBACK WHALES ALONG THE PACIFIC COAST OF COLOMBIA

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Reports of humpback whale, *Megaptera novaeangliae*, mortality and harassment in Pacific waters of Colombia from 1986-2000 were analysed to determine annual frequency, location, month of occurrence, age class and potential cause. Of the 24 records, 4 were published reports and 20 collected by the authors. Significantly more animals were found dead or entangled during the 1996-2000 period ( $n = 18$ ), than previous years 1986-1990 and 1991-95 ( $n = 6$ ). Of all deaths and harassments 54.2% were calves, 41.7% adults and 4.2% juveniles, with the number of calves being significantly high, considering that the calf vs adult population ratio was consistent with 3:7 hypotheses. Deaths/harassments were more common in the Negritos Banks area (54%), followed by the Gorgona-mainland (21%), Bahía Solano-Utría sound (12.5%) and other areas (12.5%). Greatest incidence (87.5%) was in the second half of the year: August ( $n = 6$ ), September ( $n = 5$ ) and October ( $n = 6$ ). Two calf strandings were recorded early in the year, one in February and one in April and probably originated from the Northern Hemisphere population. Annual frequency of occurrence over the 15-year period indicates an increasing trend of entanglement and vessel strike since 1996. For 24 reported events the cause of death was unknown in 9 and of the remaining 15, 1 was from natural causes with 14 showing signs of anthropogenic influence: 10 entangled, 3 from vessel strike and 1 exhibiting marks consistent with a hunting attempt. □ Colombia, humpback whale, harassment, death, entanglement, vessel strike.

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Cetacean research in Colombia is recent compared with other South American countries (Vidal, 1990; Flórez-González & Capella, 1995). There are no records of strandings or bycatches of great whales prior to the early 1970s (Vidal, 1990; Fundación Yubarta, unpubl. data), but some general commercial whaling data exist from the tropical eastern Pacific. Between the 18th and 19th Centuries, American whalers hunted sperm (*Physeter macrocephalus*) and baleen whales, mainly humpback whales (*Megaptera novaeangliae*), largely from the Galapagos Islands and in the Panamá Bay Bank, along a deep-water belt from the coast of Darién in Colombia to the Gulf of Chiriquí in Panamá (Townsend, 1935). Information from the Pacific coast of Colombia is sparse with sightings of humpback whales first mentioned by Brown (1905), and subsequently by Clarke (1962), Alberico (1986) and Flórez-González (1989).

Humpback whales, world-wide, migrate annually from high latitude, cold-water feeding grounds to tropical waters for breeding and calving (Mackintosh, 1965; Dawbin, 1966; Clapham & Mead, 1999). Distribution and

migratory movements of humpback whales in the western seas of South America are known from whaling records, occasional sightings and recently from the identification of individual animals (Townsend, 1935; Mackintosh, 1965; Aguayo, 1974; Flórez-González, 1989; Stone et al., 1990; Gibbons et al., 1998). Humpback whales feed along the western Antarctic Peninsula during summer of the Southern Hemisphere (Stone & Hamner, 1988; Stone et al., 1990) and in winter migrate to breeding grounds along the coast of Colombia and Ecuador (Flórez-González et al., 1998).

Annually, from June - November, humpback whales visit the near-shore waters of the Colombian Pacific for rearing of calves and breeding (Flórez-González, 1991; Flórez-González & Capella, 1993). Sightings in oceanic waters are rare during the breeding season (Wade & Gerrodette, 1993; Gerrodette & Palacios, 1996). Although humpback whales are distributed and migrate close to continental shores (Flórez-González et al., 1998), records of strandings and entanglements are uncommon in Colombia. Prior to 1986 no data were available.

but in recently considerable numbers have been documented along Colombia's Pacific coast. In this paper, we review the limited published records and other information on deaths and entanglements of humpback whales to determine annual frequency, spatial distribution and age classes involved. Apparent causes of mortality and harassment of whales were also examined.

## METHODS

**STUDY AREA.** The study covered beaches and near-shore waters along the Pacific coast of Colombia, extending to the borders of Ecuador and Panamá (DIMAR, 1988), and waters surrounding the offshore islands of Gorgona (02°58'N, 78°11'W) and Malpelo (03°58'N, 81°35'W) (Fig. 1).

**DATA COLLECTION.** Data of deaths (stranding, floating dead or osteological remains) and entanglements were obtained by Fundación Yubarta researchers, mainly during fieldwork of an ongoing study, from 1986. Information provided by locals was confirmed and augmented, in some cases involving travel to specific sites and in other cases analyses of photographs, videotapes or written reports. Mostly the 'cause' of death was established by observation of the carcass and not from necropsy. Available literature was also reviewed for records of strandings and osteological remains.

**ANALYSES.** The following data were recorded for each dead, entangled or otherwise harassed whale (i.e. with traces of nets on body from recent non-lethal entanglement): date, location, body length (or estimate), gender (if known), estimated age class and the presence of body markings or net remains indicating possible anthropogenic cause. Years are not listed where no deaths or entanglements were reported. Where body length was not recorded, report notes and other published parameters taken from whale catch data were used to infer the age class. Animals <8.0m in length were defined as 'calf' and presumed to be a calf of the year (Chittleborough, 1959; Nishiwaki, 1959; Clapham & Mead, 1999). Whales measuring between 8.0-12.0m were classed as 'juvenile' (Nishiwaki, 1959; Clapham, 1992, 1994) and animals >12.0m as 'adult' and considered to be sexually mature (Nishiwaki, 1959; Rice, 1963; Clapham, 1992).

Two seasons, summer and winter, are distinguished here: 'summer' is considered as January to June (corresponding to the summer and

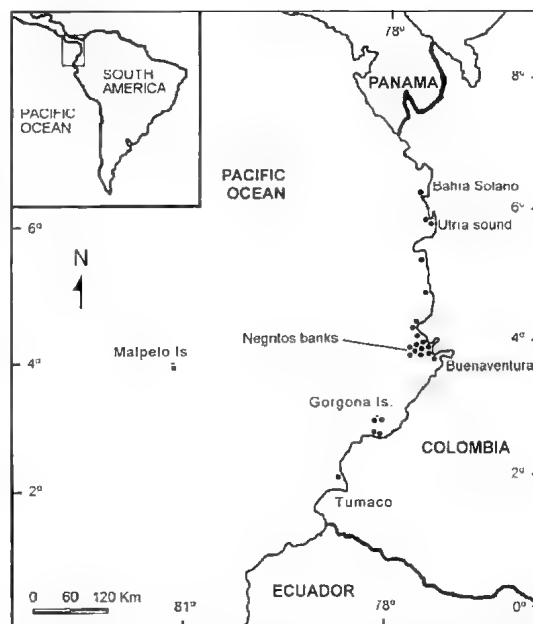


FIG. 1. Map of Pacific coast of Colombia showing the locations (solid dots) of the reported cases of death and harassment (by entanglement) of humpback whales from 1986-2000.

autumn seasons in the Southern Hemisphere) and 'winter' as July to December (winter and spring).

Factors relating to mortality or harassment were obtained from on-site examination by investigators of Fundación Yubarta, or from written reports or photographs. Where on-site records made reference to net fragments on the body, rope marks, large cuts, propeller marks or broken bones, we attributed the death or harassment event to possible anthropogenic causes (entanglement, ship strike or possible intended hunting). Deaths that showed no indication of human interaction were grouped into a category of 'natural' death (Wiley et al., 1995). Osteological remains or carcasses reported in an advanced stage of decomposition were considered as 'unknown' cause of death.

## RESULTS

Data on 24 cases of death or harassment of humpback whales were gathered between 1986-2000 (Table 1). Four were reported by Mora & Muñoz (1994), the first Colombian record consisting of osteological remains of an adult in 1986. Of the incidents recorded, 75% (18/24) occurred from 1996 onwards, while only three were reported during each of the periods 1986-90

and 1991-95. Due to the small size of the sample, statistical analyses should be regarded with caution even when significant differences appear. The number of dead and entangled whales was significantly greater in the period between 1996-2000 ( $n = 18$ ), than the 1986-90 (Mann-Whitney,  $U = 25.0$ ,  $P < 0.01$ ), 1991-95 (Mann-Whitney,  $U = 25.0$ ,  $P < 0.01$ ) and 1986-1995 (Mann-Whitney,  $U = 50.0$ ,  $P < 0.001$ ) periods pooled together ( $n = 6$ ). Although there were two 2-year periods of no reported incidents (1988-89 and 1994-95), the annual frequency of occurrence over the 15-year period indicates an increased trend of entanglement and death since 1996.

Three incidents were not included in the monthly occurrence analysis (Nos 1, 3 and 6, Table 1), these being osteological remains or of mummified bodies, which prevented determination of the date of death to the month level. There were significantly more deaths and entanglements (90.5%) during winter (second half of the year) with only two cases (9.5%) during summer (Fig. 2) (Mann-Whitney,  $U = 36.0$ ,  $P < 0.005$ ). Greatest frequencies were in August ( $n = 6$ ) and October ( $n = 6$ ) followed by September ( $n = 5$ ), accounting for 80.9% of all incidents.

Based on the inferred age classes, 54.2% ( $n = 13$ ) were calves of the year, 41.7% ( $n = 10$ ) adults and 4.2% ( $n = 1$ ) juveniles (Table 1). Pooled yearly data showed the number of deaths and entanglements of calves and adults was not significantly different from parity ( $G$ -statistic,  $G = -31.492$ ,  $P > 0.9$ ). When compared with the 3:7 (calves vs adults) hypothesis (the highest ratio found within the Colombian Pacific breeding sites [Bravo et al., 1994; Celis, 1995; Flórez-González et al., 1997]), a real age class ratio showed the number of dead and entangled calves was significantly larger than that of adults during the study period ( $G$ -statistic,  $G = 6.944$ ,  $P < 0.01$ ). Since 1996, 66.7% ( $n = 12$ ) of the 18 incidents documented involved calves. Gender information was available only for five whales; four female and one male.

The greatest incidence of death and/or entanglement occurred in Negritos Banks and surrounding area (Fig. 1) with 13 cases (54%), followed by 5 in the Gorgona Island-mainland area (21%), 3 in the Bahía Solano-Utría Sound area (12.5%) and others (12.5%). Of the 24 reported cases, 10 were entanglements, of which 2 drowned and 8 had unknown outcomes. Three of the entangled whales with unknown outcomes

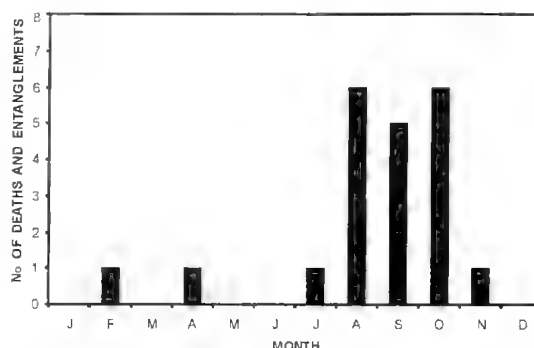


FIG. 2. Number of deaths and entanglements of humpback whales per month reported along the Pacific coast of Colombia, 1986-2000.

were released alive or partially disentangled after human intervention (Table 1). Of the 24 animals documented, 9 were eliminated from analysis of potential cause of death: 3 being osteological remains and 6 in partial or advanced stage of decomposition. Of the remaining 15, 3 (20.0%) had injuries potentially attributed to vessel strikes, 10 (66.7%) were entangled, 1 (6.7%) exhibited marks consistent with hunting attempts and 1 (6.7%) died of natural causes. Thus, 93.3% of the sufficiently inspected whales showed signs that anthropogenic factors may have contributed to, or have been directly responsible for, the death or harassment (and potential death).

## DISCUSSION

The results indicate that deaths and harassments of humpback whales along the Pacific Colombian coast have increased since 1986, principally between 1996-2000 (75%). It is likely that the actual incidence of death and entanglement (directly lethal or not) could be higher, since not all dead humpback whales wash ashore, nor are live disentangled whales always observed (as evidenced by whales with pieces of net attached). Possible explanations for the apparent increase in deaths and entanglements include the growth of the humpback whale population, increase in mortality factors and in observation efforts. This last factor seems unlikely as the authors obtained the majority of records during a long-term study on breeding of humpback whales begun in 1986 and fieldwork effort has been equal from year to year. If the reported increase in deaths and entanglements were due to increased observer effort, an increased incidence of these events for other great whales should also be expected. However strandings or entanglements of sperm whales and Bryde's whales (*Balaenoptera edeni*)

TABLE 1. Records of deaths and harassments of humpback whales along the Pacific coast of Colombia, 1986-2000.

No.	Date	Locality	Position	Age class	Length (m)	Sex	Remarks, Carcass Analyses	Cause of death or harassment	Source
1	23.08.86	Cuevita bay	05°24'N 77°25'W	Adult	-	?	Osteological remains	Unknown	Mora & Muñoz (1994)
2	.09.87	Malpelo island	03°56'N 81°34'W	Juvenile	~10	?	Floating dead, with marks of harpoon	Hunt	This study
3	23.12.90	Usagará	04°50'N 77°22'W	Adult	-	?	Osteological remains	Unknown	Mora & Muñoz (1994)
4	.09.92	Puerto España	04°00'N 77°25'W	Adult	-	?	Stranded dead. No external injuries noted	Natural	Mora & Muñoz (1994)
5	15.02.93	Bahía Solano	06°15'N 77°25'W	Calf	3.5-4.0	?	Floating dead, partially decomposed	Unknown	This study
6	.06.93	Salahonda	02°05'N 78°42'W	Adult	-	?	Osteological remains	Unknown	Mora & Muñoz (1994)
7	.08.96	Negritos Banks	03°55'N 77°25'W	Calf	~6	?	Disentangled alive from gillnet	Entanglement	This study
8	11.08.96	Negritos Banks	03°55'N 77°25'W	Adult	~16	?	Alive with net around mouth, survival unknown	Entanglement	This study
9	.09.96	Gorgona island	03°00'N 78°12'W	Calf	~7	♂	Floating dead, partially decomposed	Unknown	This study
10	19.10.96	Negritos Banks	03°55'N 77°25'W	Adult	16	♀	Alive with net around mouth, survival unknown	Entanglement	This study
11	19.10.96	Negritos Banks	03°55'N 77°25'W	Calf	6	?	Alive with net around mouth, survival unknown	Entanglement	This study
12	14.07.97	Chicoperez	02°50'N 78°22'W	Calf	6	♀	Dead in a gillnet	Entanglement	This study
13	.08.97	near Gorgona Is	03°05'N 78°20'W	Calf	~6	?	Disentangled alive from purse seine	Entanglement	This study
14	.09.97	Charambirá	04°17'N 77°30'W	Adult	>13	?	Stranded dead, partially decomposed	Unknown	This study
15	28.10.97	Ladrilleros	03°56'N 77°22'W	Calf	5.2	♀	Stranded dead. Two areas of hemorrhage noted	Vessel strike	This study
16	21.04.98	Utria Sound	06°05'N 77°22'W	Calf	~5	?	Stranded dead. Propeller cuts on caudal peduncle	Vessel strike	This study
17	02.10.98	Del Tigre Sound	03°52'N 77°18'W	Calf	~7	?	Floating dead. Advanced decomposition	Unknown	This study
18	15.11.98	Del Tigre Sound	03°52'N 77°18'W	Calf	6	?	Floating dead, partially decomposed	Unknown	This study
19	17.08.99	Charambirá	04°17'N 77°30'W	Adult	>13	?	Stranded dead, partially decomposed	Unknown	This study
20	20.08.99	Piangüita	03°50'N 77°10'W	Adult	16.5	♀	Stranded dead. Right mandible fractured, cuts on peduncle	Vessel strike	This study
21	04.10.99	Utria Sound	06°05'N 77°22'W	Calf	5	?	Dead in a gillnet	Entanglement	This study
22	22.08.00	Negritos Banks	03°55'N 77°25'W	Calf	6	?	Alive with net around head, survival unknown	Entanglement	This study
23	30.09.00	Mulatos	02°40'N 77°25'W	Adult	>13	?	Disentangled alive from gillnet	Entanglement	This study
24	15.10.00	Negritos Banks	03°55'N 77°25'W	Calf	~5	?	Alive with net around mouth, survival unknown	Entanglement	This study

have remained relatively constant and low in Colombia for the same period (Fundación Yubarta, unpubl. data).

Increase in deaths and entanglements may be due to an increase in the number of animals inhabiting the study area, or an increase in human

activity (i.e. vessel traffic, expansion of gillnet and purse seine use), or both. Recent humpback whale estimates show a significant increase in the population wintering in Colombian waters during the decade 1986-95, from a mean size of 173 (Flórez-González, 1991) to 1,495 (Capella et

al., 1998), an increase of 764%. Although the population size estimated for both the Negritos Banks (mean 857, 95% CI 547-1167) and Gorgona Island area (mean 1495, 95% CI 919-2071) is not different (Capella et al., 1998), greater densities are also typically found in the Negritos Banks area as compared with other breeding sites on the Pacific coast of Colombia (Flórez-González et al., 1997). The annual frequency of deaths and entanglements rose sharply in 1996, with no evidence before then. The highest frequency occurred in the surrounding waters of the Negritos Banks on the central coast of Colombia. Notably, 61.5% (8/13) of the deaths and entanglements reported since 1996 in this area were related to human activity, including vessel strike and entrapment in gillnets or active fishing gear. These factors represent an increased hazard to animals seasonally inhabiting this area. The Buenaventura harbour, a few kilometers south of Negritos Banks, is the main fishery and commercial shipping port on the Colombian Pacific coast. Artisanal gillnet fishing is important in the coastal waters around the Bahía Málaga and Negritos Banks (pers. obs.), as is a growing commercial traffic of whale watching vessels that commenced in 1994 (Pardo, 2000; Fundación Yubarta, unpubl. data).

Monthly distribution of humpback whale deaths and entanglements was not restricted to the second half of each year, although it was most frequent from August-October (Southern Hemisphere winter), when the species occupancy reaches peak levels in near-shore waters of the Colombian Pacific (Flórez-González & Capella, 1993; Soler, 1996; Suárez, 2000). One early calf death was reported in February and one in April, (winter months of the Northern Hemisphere). These two calves were found on the north coast of Colombia and probably belonged to the North Pacific humpback whale population that breeds from Mexico to Costa Rica (Urbán & Aguayo, 1987; Steiger et al., 1991; Rasmusen et al., 1995). Few sightings of humpback whales have been reported for the northern coast of Colombia during the first half of the year (Fundación Yubarta, unpubl. data). These records are consistent with findings from genetic studies (Baker et al., 1990, 1998) and support consideration of this region as a potential site for exchange between hemispheres (Flórez-González et al., 1998).

Since humpback whales are more commonly found in coastal waters (Flórez-González, 1991; Flórez-González & Capella, 1993), they are more exposed to vessel traffic and various types of

fishing gear. Although the cause of death in 9 (37.5%) reported cases was not determined, a significant portion (58.3%) of deaths or harassments were related to human factors, principally vessel strike and entanglement as gillnet bycatch. About 3% of humpback whales identified in Colombian waters show holes, scars, or deep cuts on the body, evidence from ship strikes and propeller cuts without immediate lethal consequences (Fundación Yubarta, unpubl. catalogue). Our results are consistent with research in other humpback whale breeding and feeding grounds which frequently implicate human-related activities (mostly bycatch entrapments) to whale deaths (Wiley et al., 1995; Félix et al., 1997; Mazzuca et al., 1998; Weinrich, 1999) and that fishing gear entanglements are a highly significant threat (Perkins & Beamish, 1979; Heyning & Lewis, 1990; NMFS, 1991; Perrin et al., 1994).

Recent reports of humpback whale deaths and entanglements are disproportionately high for calves of the year, indicating that this portion of the population should be an important focus for management in Colombia and the southeast Pacific. Although the cause of death of some stranded whales could not be certain, activities such as irresponsible whale watching may have contributed to mortality. Calves have been temporarily separated from their mothers through harassment from whale watching vessels (pers. obs.) and such 'disorientated' calves, or newly weaned calves, may be susceptible to entanglement in nearby nets. Information on calf mortality is a critical parameter to determine recruitment rates and its quantification is essential for assessing the rate of recovery of this vulnerable species. The rate of neonatal mortality in the Pacific waters of Colombia has not yet been quantified.

While the current rate of mortality from human related activities (fishing gear or vessel strike) does not appear to seriously threaten this stock of humpback whales, it may slow its' population recovery. The susceptible status of this species and its affinity for near shore habitats increase concern. Collective effects of industrial development, resource exploitation and rapid increase in the whale watching industry could result in displacement and habitat degradation and impact on population numbers. Although the whale watching industry in Colombia was regulated in 1997, control exercised by local authorities is rather weak. Reasonable efforts to reduce the cause and rates of ship collision and entanglement must be developed to successfully minimise

their effects. The establishment of such measurements has been recommended world-wide (NMFS, 1991; Perrin et al., 1994).

This study indicates that incidental mortality and harassment of humpback whales in Colombia are a problem for their conservation. Management of fisheries, whale watching activities and ship traffic in specific areas must be addressed.

#### ACKNOWLEDGEMENTS

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**RECENT FINDINGS CONCERNING THE MIGRATION AND BREEDING GROUND COMPOSITION OF NORTH ATLANTIC HUMPBAC WHALES.** (ABSTRACT) During 1992 and 1993, the North Atlantic humpback whale (*Megaptera novaeangliae*) was studied throughout its known range in an international project known as the Years of the North Atlantic Humpback (YONAH). Using standardised searching and sampling methodologies, the study collected an unprecedented number of fluke identification photographs (n=3,001 unique individuals) and skin biopsies (n=2,105 unique individuals) in both the summer feeding grounds and winter breeding grounds. In addition, the samples were compared to the Gulf of Maine life history catalog (871 unique individuals, 224 of known age in 1993), maintained by the Center for Coastal Studies. An analysis of the sex, age, feeding ground origin and timing of identified individuals on the breeding ground produced new discoveries about the migration of North Atlantic humpback whales. These include evidence that a significant number of juvenile whales do not

migrate. Moreover, although the operational sex ratio is skewed towards males, most mature females do migrate, but, unlike males, they show a significant individual, between-year consistency in the timing of their arrival on the breeding ground. This timing appears to be independent of their reproductive status. In addition, results show for the first time that eastern and western North Atlantic animals share a common breeding ground, however, they do not entirely overlap in time, as those from Iceland and Norway arrive on average later in the winter season. Several of these findings appear to be inconsistent with some historic and modern findings from the southern and the north Pacific Oceans. Several possible explanations are discussed.

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**HUMPBAC SONG AND NON-SONG: PATTERNS, SOURCE-LEVELS, LEARNING AND ATTRACTION TO BREACHING SOUNDS.** (ABSTRACT) Humpback whales (*Megaptera novaeangliae*) have a well known, less well understood, singing behaviour. They produce a repertoire of sounds not associated with song. Based on observations from the east and west Australian coast, characteristics of humpback whale vocalisations are presented. The 1994 east coast song was made up of 31 components for a length of 6-10 minutes. Components were mostly centred about the 315 or 400Hz 1/3 octaves but ranged from 25-2500Hz and had peak-peak source levels which ranged over 171-196dB re 1 $\mu$ Pa at one metre. The source level of the same component was seen to vary by up to 14dB (peak-peak) and 0.46s in total length. Some sounds seemed adapted for short range transmission only (< 1km) whereas others seemed better adapted for longer range transmission (many kms). In tropical Australian breeding grounds it was normal that several singers, often at short range, were heard at

any one time. In some instances apparent 'jousting' occurred, where the songs of two singers at similar ranges stayed in step. An instance believed to be a yearling being taught by a 'songmaster' was observed. The believed yearling song was peppered with mistakes and often jumped phrases to keep up with the other. Non-song vocalisations have correlated with aggression, cow-calf or cow-yearling interactions and breaching events. Signals produced during breaching events show strong similarities with impulsive air-gun signals used in petroleum exploration. In trials carried out with an air-gun, believed male humpback whales were attracted to a repetitive air-gun signal, with speculation that the similarity to a breaching signal was the stimulus.

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**CETACEAN CONSERVATION: A NATIONAL PERSPECTIVE.** (ABSTRACT) The Commonwealth of Australia has been administering the *Whale Protection Act 1980* to protect cetaceans for the past twenty years. The legislation was developed and implemented following the decision to halt whaling in Australian waters. It arose primarily out of concern for the possible extinction of a number of the great whale species that had been seriously over-exploited, and came at a time when few if any had ever considered the potential benefits of the non-consumptive uses of whales.

In 2000 that Act, among others, has been repealed and replaced by the *Environment Protection and Biodiversity Conservation Act 1999* (EPBC Act), which brings Australia's environmental legislation up to date. The Act establishes the Australian Whale Sanctuary in recognition of the high level of

protection afforded to cetaceans. It also heralds some major changes in the management of the marine environment, especially in relation to the approval of actions that may affect cetaceans.

This year has also seen the 52nd annual meeting of the International Whaling Commission held in Australia. The Commonwealth Government continues to advocate a policy opposing all commercial and 'scientific' whaling. As part of a goal of establishing a global sanctuary for whales, Australia jointly sponsored the proposal for a South Pacific Whale Sanctuary, which was put to the Plenary meeting for consideration.

Robyn McCulloch (e-mail: robyn.mcculloch@ea.gov.au) and Milena Rafic, Environment Australia, PO Box 787, Canberra 2601, Australia; 29 August 2000.

PHOTO-IDENTIFICATION OF HUMPBACK WHALES, *MEGAPTERA NOVAEANGLIAE*, OFF THE ANTARCTIC PENINSULA: 1997/98 TO 1999/2000

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Dalla Rosa, L., Secchi, E.R., Kinan, P.G., Santos, M.C.O., Martins, M.B., Zerbini, A.N. & Bethlem, C.B.P. 2001 12 31: Photo-identification of humpback whales, *Megaptera novaeangliae*, off the Antarctic Peninsula: 1997/98 to 1999/2000. *Memoirs of the Queensland Museum* 47(2): 555-561. Brisbane. ISSN 0079-8835.

During three summer seasons (1997/98-1999/00), photographic sampling of humpback whales was conducted by Projeto Baleia/Brazilian Antarctic Programme in waters of the Antarctic Peninsula. Whales photographed totalled: 63 (1997/1998), 70 (1998/1999) and 21 (1999/2000). Of these, 74.6% (n = 47), 87.1% (n = 61) and 100% (n = 21), respectively, were represented by photographs categorised as quality 1 (excellent) or 2 (moderate). Inter-annual comparisons showed two matches: a whale photographed on 27 January 1998 in the Gerlache Strait was resighted on 11 January 1999 in the same region; the second on 3 February 1998 in the Gerlache Strait was resighted on 25 January 1999 at almost the same coordinates. These matches indicate that humpback whales may show fidelity to feeding grounds off the Antarctic Peninsula. Intra-annual comparisons showed two matches: a whale photographed on 22 January 1998 close to the King George Island and another on 27 January 1998 in the Bismarck Strait were resighted together on 7 March 1998 in the Gerlache Strait. Average indices of fluke colouration obtained for 1997/1998 and 1998/1999 were 2.39 (n = 44) and 2.60 (n = 53), respectively. Total average index, including photographs from the three periods, resulted in 2.54 (n = 116). All values are significantly different from those obtained by Rosenbaum et al. (1995) for western and eastern Australia (p < 0.001) and similar to that found for Colombia (p > 0.05) (non-parametric test of Kolmogorov-Smirnov). These results reinforce the view that humpback whales feeding in the western side of the Antarctic Peninsula probably originate from eastern South Pacific breeding grounds. □ *Humpback whale, photo-identification, fluke pigmentation patterns, Antarctic Peninsula.*

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Katona et al. (1979), Whitehead et al. (1980) and Katona & Whitehead (1981) pioneered photo-identification studies based on variation in ventral fluke pigmentation of humpback whales, *Megaptera novaeangliae*. Since then, photo-ID techniques have provided information on many aspects of life history, abundance, distribution, movements and migratory patterns of humpback whales worldwide (e.g. Whitehead et al., 1983; Baker et al., 1986; Clapham & Mayo, 1987; Calambokidis et al., 1990; Katona & Beard, 1990; Kaufman et al., 1990; Perry et al., 1990; Kinan & Bethlem, 1998; Smith et al., 1999; Steiger & Calambokidis, 2000).

Recent studies in molecular biology (e.g. Baker et al., 1994; Valsecchi et al., 1997) and pigmentation patterns/photo-ID (e.g. Rosenbaum et al., 1995; Stone et al., 1990) have not determined stock discreteness of Southern Hemisphere humpback whales. Catalogue comparisons from breeding and feeding grounds showed no matches between whales in the Brazilian wintering ground (n = 80) and the Antarctic Peninsula (n = 233) (Muñoz et al., 1998), although significantly more humpback whales have since been photo-identified in the Brazilian area (~475: Bethlem, 1998).

The Projeto Baleia, part of the Brazilian Antarctic Programme (PROANTAR), has carried out

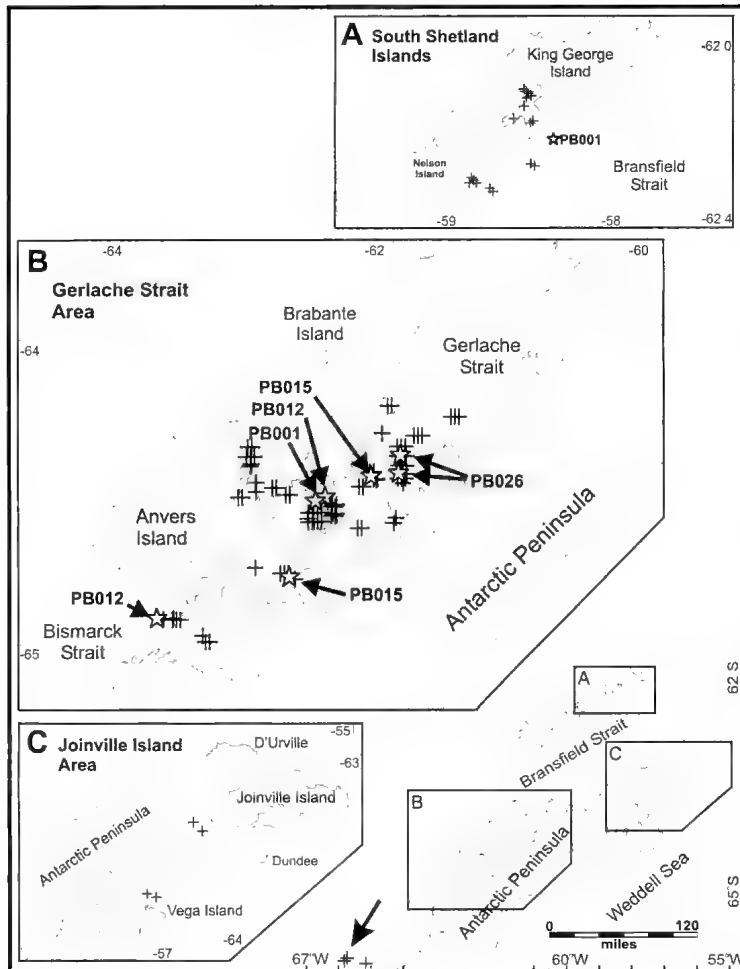


FIG. 1. Study area off the Antarctic Peninsula. The points indicate sighting positions of humpback whales photo-identified from 1997/1998 to 1999/2000.

photo-ID recording and genetic biopsy sampling of humpback whales for genetic and pollution analyses, and cetacean density estimates in the Antarctic Peninsula region to improve knowledge of Southern Hemisphere cetacean stocks.

In this preliminary study, we make inter- and intra-annual comparisons and calculate average colouration indices of humpback whales photo-identified in the Antarctic Peninsula region.

#### MATERIAL AND METHODS

**FIELD WORK.** During three summer seasons (1997/1998-1999/2000), ship surveys for biopsy and photo-ID of humpback whales and for cetacean density estimates were conducted from the 75m Oceanographic and Supply Ship (NAPoc) 'Ary

Rongel', in waters off the Antarctic Peninsula (IWC areas I and II) (Fig. 1). The main survey sites were the Gerlache Strait and the South Shetland Islands. Data were mostly collected on a time-opportunity basis according to the PROANTAR's schedule, however dedicated surveys were performed in the Gerlache Strait, where they were divided between biopsy/ photo-ID and density estimate studies.

Searches were made from the exterior wing bridges, approximately 14m above sea level, unless weather conditions forced the observers to watch from the bridge. When time and weather conditions were favourable, a small inflatable boat was launched to approach and photo-identify humpback whales. Otherwise, photo-ID was performed from the wing bridges and the bow of the ship, when approaches were possible.

Usually three scientists manned the inflatable; one responsible for photographing, another for biopsy sampling or photographing, and the third for recording data and assisting with films and biopsy samples. Each whale was photographed recording the

underside of the fluke and both sides of the dorsal fin, wherever possible. Photographs were taken with 35mm SLR cameras equipped with 75-300mm zoom or 300mm telephoto lenses. Preference was given to colour print films ISO 200 and 400, usually the latter for its performance under most light conditions. Slide films ISO 100-400, black-and-white T-Max 400 (pushed or not) and colour print films ISO 100 were occasionally used.

Data recorded during photo-ID included: sighting date, time, coordinates (recorded on the ship's GPS), pod size, calf presence, photographer, films, frames taken, corresponding biopsy numbers when available, and any additional relevant observations. Conspicuous

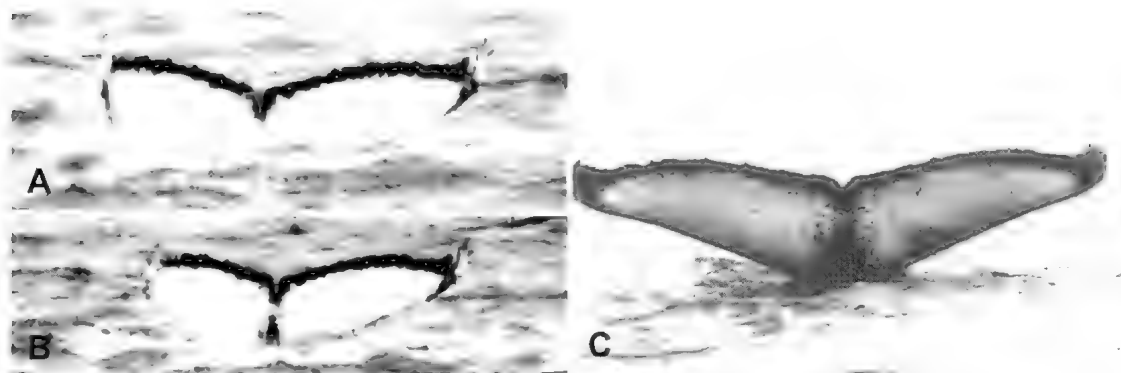


FIG. 2. Ventral fluke photographs of whale PB015 taken on 27 January 1998 (A & B) and 11 January 1999 (C) in the Gerlache Strait, Antarctic Peninsula.

natural markings, especially on the flukes and dorsal fins, were drawn on a datasheet for field reference.

**ANALYSIS OF FLUKE PHOTOGRAPHS.** Each photographed whale received a reference code based on the order of observation in a season (e.g. OA16/PB01). The best available fluke photograph of each individual on each observation was analysed and rated from 1 to 3 according to photo quality and recognition quality, following Mizroch et al. (1990): 1 (excellent), 2 (moderate), 3 (poor). Complementary photographs were considered for fluke information when necessary. Whales identified by photographs rated 1 or 2 in photo quality were included in the main catalogue and received an overall identification code (e.g. PB001).

Photographs (10 × 15 cm print size) were organised by summer season according to decreasing amounts of white pigmentation on the underside of the flukes and compared serially with the entire data set. Inter-annual comparisons examined evidence of site fidelity to the feeding grounds around the Antarctic Peninsula, while intra-annual comparisons examined time of residency and movements of humpback whales in the area during feeding seasons.

To examine the identity of the humpback whales stock using the area, average indices of fluke colouration were calculated according to Rosenbaum et al. (1995) and compared to indices available from Southern Hemisphere breeding grounds, using the non-parametric test of Kolmogorov-Smirnov (Zar, 1996). Photographs of quality 1 and 2 from whales photographed on the western side of the Antarctic Peninsula were assigned rank values on a scale of 1 (white) to 5 (black) based on the proportion of pigmentation

present on the underside of the flukes (see also Carlson et al., 1990). These scores were multiplied by the frequency of animals in each class to obtain the average index.

## RESULTS AND DISCUSSION

Season totals of humpback whales photographed were: 63 (1997/1998), 70 (1998/1999) and 21 (1999/2000), of which 74.6% ( $n = 47$ ), 87.1% ( $n = 61$ ) and 100% ( $n = 21$ ), respectively, were represented by photographs categorised as quality 1 or 2. From this set of photographs ( $n = 127$  whales, considering  $n = 2$  resights), 81.1% of the identified whales were classified as being of recognition quality 1 or 2, based on pigmentation patterns. Of these, 73.2% ( $n = 93$ ) were photographed in the Gerlache Strait and surrounding areas. Most poor quality photographs ( $n = 25$ ) were taken from the ship (76%) and were usually related to low definition due to distance, however, some showed enough information to be included in the comparisons.

Sighting positions of photo-identified humpback whales are plotted in Fig. 1, excluding one animal photographed southeast of the South Orkney Islands.

**INTER-ANNUAL COMPARISONS.** Two identified humpback whales were sighted in more than one season. One (PB015) was first sighted on 27 January 1998 in the Gerlache Strait ( $64^{\circ}27'S$ ,  $62^{\circ}10'W$ ) and again on 11 January 1999 in the same region ( $64^{\circ}47'S$ ,  $62^{\circ}45'W$ ) (Fig. 2A-C); the second (PB026) on 3 February 1998 in the Gerlache Strait (ca.  $64^{\circ}23'S$ ,  $61^{\circ}56'W$ ) and again on 25 January 1999, almost at the same coordinates ( $64^{\circ}26.4'S$ ,  $61^{\circ}55.8'W$ ) (Fig. 3A-B). These matches indicate that animals may show temporal fidelity to particular feeding

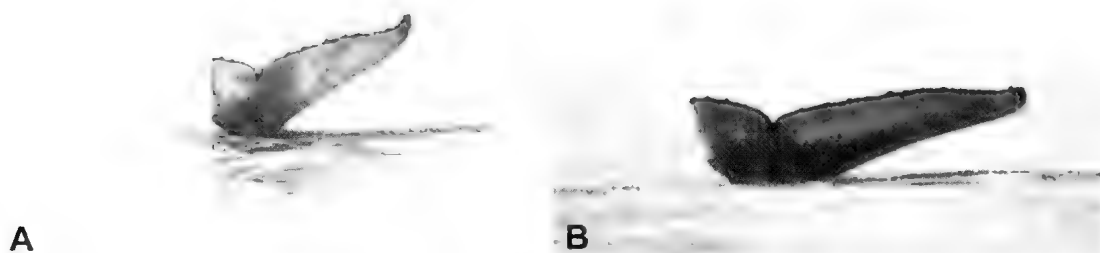


FIG. 3. Ventral fluke photographs of whale PB026 taken on 3 February 1998 (A) and 25 January 1999 (B) in the Gerlache Strait, Antarctic Peninsula.

grounds of the Antarctic Peninsula region, however a continued effort is required for verification. Five to six distinct feeding areas have been suggested for Antarctic waters (Mackintosh, 1942; Dawbin, 1966), although tag recoveries indicate some interchange among them (Dawbin, 1966).

Compiling data from long-term photo-ID studies, Katona & Beard (1990) have observed separate feeding aggregations in the western North Atlantic, and that individual whales returned annually to a particular feeding region. In the North Pacific, humpback whales also appear to form geographically isolated feeding herds (Perry et al., 1990), with little movement among feeding regions across years (Baker et al., 1986).

**INTRA-ANNUAL COMPARISONS.** Two identified humpback whales were resighted in a season. One (PB001) was sighted on 22 January 1998 close to the King George Island (ca. 62°12'S, 58°13'W) (Fig. 4A-B), the second (PB012) on 27

January 1998 in the Bismarck Strait (ca. 64°53'S, 63°45'W), near the southern end of Gerlache Strait (Fig. 5A-B). These two whales were resighted together on 7 March 1998 in the Gerlache Strait (64°31'S, 62°31'W). The whale PB012 was ~45 nautical miles from the previous sighting, indicating that individuals may remain in an area for some time during a given feeding season.

In Antarctic waters weather conditions change rapidly and humpback whales may prefer sheltered waters where sea conditions are less severe than in open waters. Dolphin (1987) reported that humpback whales would usually rest at the surface on feeding grounds. Montú et al. (1994) found high concentrations of krill in the Gerlache and Bransfield Straits. The Gerlache Strait is a protected area between Brabante and Ambers Islands and the Antarctic Peninsula, which might shelter and supply abundant food (krill, *Euphausia superba*) for the species.

Food abundance might be a factor of the ecological importance of the Gerlache Strait to

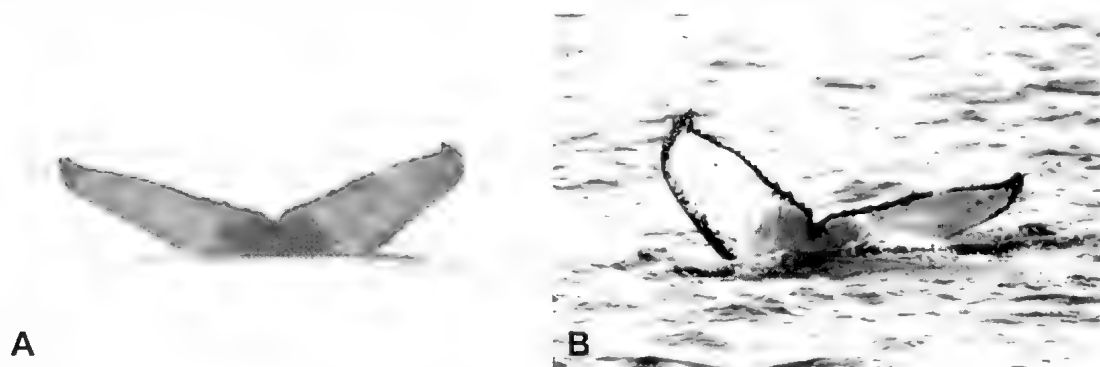


FIG. 4. Fluke photographs of animal PB001 taken on 22 January 1998 off the King George Island (A) and on 7 March 1998 in the Gerlache Strait (B), Antarctic Peninsula.

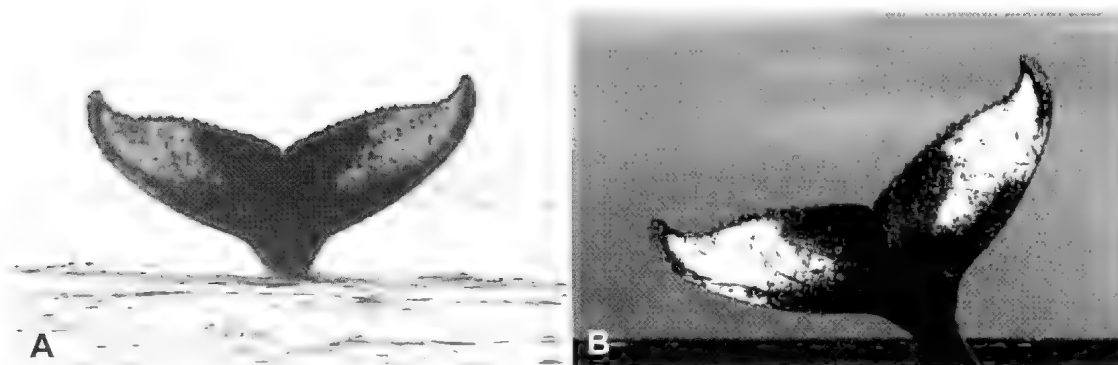


FIG. 5. Fluke photographs of animal PB012 taken on 27 January 1998 in the Bismarck Strait (A) and on 7 March 1998 in the Gerlache Strait (B), Antarctic Peninsula.

humpback whales, as evidenced by the high encounter rates (Secchi et al., 2001) and the resightings presented in this paper. Further studies are necessary to investigate local movements and seasonal residency in this area.

**COLOURATION INDICES.** Average indices of fluke colouration for the summers 1997/1998 and 1998/1999 were 2.39 ( $n = 44$ ) and 2.60 ( $n = 53$ ), respectively. Sample size for the summer 1999/2000 was considered too small to provide an individual index. Total average index of photographs over the three periods was 2.54 ( $n = 116$ ) (Table 1). All values are significantly different from those obtained by Rosenbaum et al. (1995) for western and eastern Australia ( $p < 0.001$ ) but similar to that for Colombia ( $p > 0.05$ ) (Kolmogorov-Smirnov test). Although average indices of fluke colouration for the humpback whales breeding in the Abrolhos Bank, northeastern Brazil, were not available for comparison, these results support the view that humpback whales feeding in the western side of the Antarctic Peninsula probably originate from eastern South Pacific breeding grounds. Indeed, Muñoz et al. (1998) reported eight matches of individuals photo-identified off the Antarctic Peninsula and the northwest coast of South America.

Further photo-ID studies and comparison with other catalogues, especially from northeast Brazil, along with genetic studies would help to elucidate stock identity and migration patterns of humpback whales found in the study area. Considering the high cost and difficulties of working in the high latitudes of the Southern Ocean, combining the efforts of research groups is desirable to optimise results.

#### ACKNOWLEDGEMENTS

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TABLE 1. Average index of fluke colouration obtained in this study (1997/1998 - 1099/2000) compared to those available for Southern Hemisphere breeding grounds. \* Source: Rosenbaum et al. (1995).

Area	Fluke colouration categories					Total (n)	Average Index
	1	2	3	4	5		
Western Antarctic Peninsula	32 (27.6%)	29 (25.0%)	26 (22.4%)	18 (15.5%)	11 (9.5%)	116	2.54
Eastern Australia*	186 (83.0%)	30 (13.4%)	6 (2.7%)	2 (0.9%)	0 (0%)	224	1.21
Western Australia*	167 (87.4%)	11 (5.8%)	6 (3.1%)	2 (1.1%)	5 (2.6%)	191	1.26
Colombia*	65 (36.1%)	41 (22.8%)	41 (22.8%)	19 (10.5%)	14 (7.8%)	180	2.31

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**A NOVEL BEHAVIOR OBSERVED IN HUMPBACK WHALES ON WINTERING GROUNDS AT ABROLHOS BANK (BRAZIL) AND THE COMOROS ARCHIPELAGO (SOUTHEASTERN AFRICA).**

(*ABSTRACT*) We describe a novel behavior, termed 'tail-up', observed in humpback whales (*Megaptera novaeangliae*) on wintering grounds on Abrolhos Bank, Brazil and in the Comoros Islands off southeastern Africa. The behaviour involves the whale positioned vertically in the water column with its tail and a portion of the caudal peduncle in the air. The length of tailing-up time between surfacings to breathe ranged from a few seconds to approximately 15 minutes. The maximum observed duration of a tail-up bout on any one day was ten hours, and some individuals engage in the behavior for two consecutive days. With the exception of calves, tail-up behaviour was observed in all classes of whale. At Abrolhos, tail-ups were recorded in 76 (5.7%) of 1,324 groups observed from a shore station, and in 215 (16.0%) of 1,343 groups observed from vessel surveys; biases in each method

suggest that the true frequency lies between these two figures. Tail-ups differ from 'sailing' behavior in southern right whales in duration and variable orientation of the whale relative to wind direction. The purpose of tail-up behavior is unknown, but its frequency and the prolonged duration of some bouts suggest that it performs an important function, perhaps related to energetics.

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**ANTARCTIC PENINSULA HUMPBACK WHALES: RELATIVE ABUNDANCE IN FIVE SUMMER SEASONS (1994/95 - 1998/99) AND MIGRATORY CONNECTIONS BASED ON PHOTO-IDENTIFICATION.**

(*ABSTRACT*) Since the austral summer 1994/95 the Chilean Antarctic Institute has supported research on cetaceans of the western coast waters off the Antarctic Peninsula (Bransfield and Gerlache Straits), focused on humpback whales. In five consecutive summers of field work, humpback whales (*Megaptera novaeangliae*) were the most abundant species after minke whales (*Balaenoptera* spp) and killer whales (*Orcinus orca*). Photo-identification allowed the identification of almost 170 whales in total without matches between the studied five years. Recaptures were obtained only in the same season showing information on local movements and short-term residence in

the feeding grounds. The comparison of ventral fluke pigmentation patterns with breeding grounds of the northern and southern hemispheres supports a close link with Colombian grounds. This phenotypic approach agrees with recent molecular data that recognise a strong migratory connection between the two historical grounds of Stock I, as has been proposed based on whaling data.

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**HUMPBACK WHALES ... STOPPING A WHILE IN HERVEY BAY.**

(*POSTER*) Queensland Parks and Wildlife Service manage and monitor human interactions near humpback whales and assist whale protection. Whale watch regulations are enforceable under the *Nature Conservation (Whales and Dolphins) Conservation Plan 1997*.

Vessel patrols educate boat users about whale watch regulations and ensure regulation compliance. Signage and brochures have been developed to provide the public with

information on the regulations in a readable and readily understandable form. Diagrams complementing the written word are also utilised as a means of providing whale watchers with clear information relating to their obligations by law when whale watching.

Sue Olsson and Moyra McRae, Queensland Parks and Wildlife Service, Environmental Protection Agency, PO Box 101 Maryborough 4650, Australia, (e-mail: Moyra.McRae@env.qld.gov.au); 29 August 2000.

## ASPECTS OF HABITAT USE PATTERNS OF HUMPBAC WHALES IN THE ABROLHOS BANK, BRAZIL, BREEDING GROUND

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Martins, C.C.A., Morete, M.E., Engel, M.H., Freitas, A.C., Secchi, E.R. & Kinas, P.G. 2001 12 31: Aspects of habitat use patterns of humpback whales in the Abrolhos Bank, Brazil, breeding ground. *Memoirs of the Queensland Museum* 47(2): 563-570. Brisbane. ISSN 0079-8835.

The Abrolhos Bank (off the State of Bahia, northeastern Brazil) is the most important breeding and calving ground for humpback whales, *Megaptera novaeangliae*, in the western South Atlantic. The area is shallow with a mean depth of 30m and a group of five islands (the Abrolhos Archipelago) is located in the northern portion of the Bank. Data collected from 1992 to 1998 were analysed to identify possible different habitat use patterns by different humpback whale group types. An analysis of variance found differences in the mean water depths where different group types were recorded: single whales, 18.9m (se = 0.505); pairs, 18.6m (se = 0.386); competitive groups, 19.1m (se = 0.573); mother-calf pairs, 15.8m (se = 0.373); mother-calf-principal escort, 14.9m (se = 0.489); and competitive group with mother-calf pair, 16.4m (se = 0.889). With the exception of competitive groups, those containing calves (mother-calf alone or mother-calf-principal escort) occurred in significantly shallower water than non-calf groups (Tukey test,  $p < 0.05$ ). In addition, groups containing calves were found significantly more often nearer the Archipelago (within 4 nautical miles) than other groups (two-sample Kolmogorov-Smirnov test,  $D = 0.139$ ;  $\chi^2 = 18.516$ ,  $p < 0.05$ ). Accordingly, a spatially stratified management scheme is recommended in order to protect mother-calf pairs from possible harassment by whale watching operations in the area. □ *Humpback whale, Megaptera novaeangliae, habitat use, Abrolhos Bank, Brazil.*

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The humpback whale, *Megaptera novaeangliae*, is a cosmopolitan migratory species (Dawbin, 1966). In summer, animals inhabit high latitude feeding grounds, migrating to breeding and calving grounds in tropical or subtropical waters in winter. These breeding grounds are generally associated with islands, offshore reef systems or continental shores (Dawbin, 1966; Whitehead & Moore, 1982; Clapham & Mead, 1999). The Arabian Sea humpback whale population is an exception that remains in tropical waters year-round (Mikhalev, 1997).

The Abrolhos Bank, Brazil, is the most important breeding and calving ground for humpback whales in the western South Atlantic (Engel, 1996; Siciliano, 1997). An increase in humpback whale sightings has been reported in the north of this area (Dórea-Reis et al., 1996; Zerbini et al., 2000). Using mark-recapture models of photo-identified whales, a population of 1,634 (90% CI, 1,379-1,887) was estimated in this area in 1995 (Kinas & Bethlehem, 1998). No positive match between whales sighted at Abrolhos Bank

and the Antarctic has been found (Projeto Baleia Jubarte, unpubl. data; Whale Research Team/Proantar, unpubl. data) and the summer destination of this population is unclear.

According to categories of Forestell & Kaufman (1995), Abrolhos is in a discovery phase of whale watching, which is opportunistically offered by SCUBA operators taking tourists to dive in the Abrolhos Marine National Park/IBAMA (Brazilian Institute of Environment and Renewable Resources). Tourist numbers have been stable, probably due to National Park management and carrying capacity regulations (Morete et al., 2000), with 14,000 visitors in 1995. Development of whale watching in the Abrolhos Bank region may be a source of economic benefit to the local community, nevertheless, its effects on animal behaviour and demographic trends should be assessed scientifically to assist planning.

This study obtained base line information on habitat use of the humpback whale population in the Abrolhos Bank breeding ground, from data

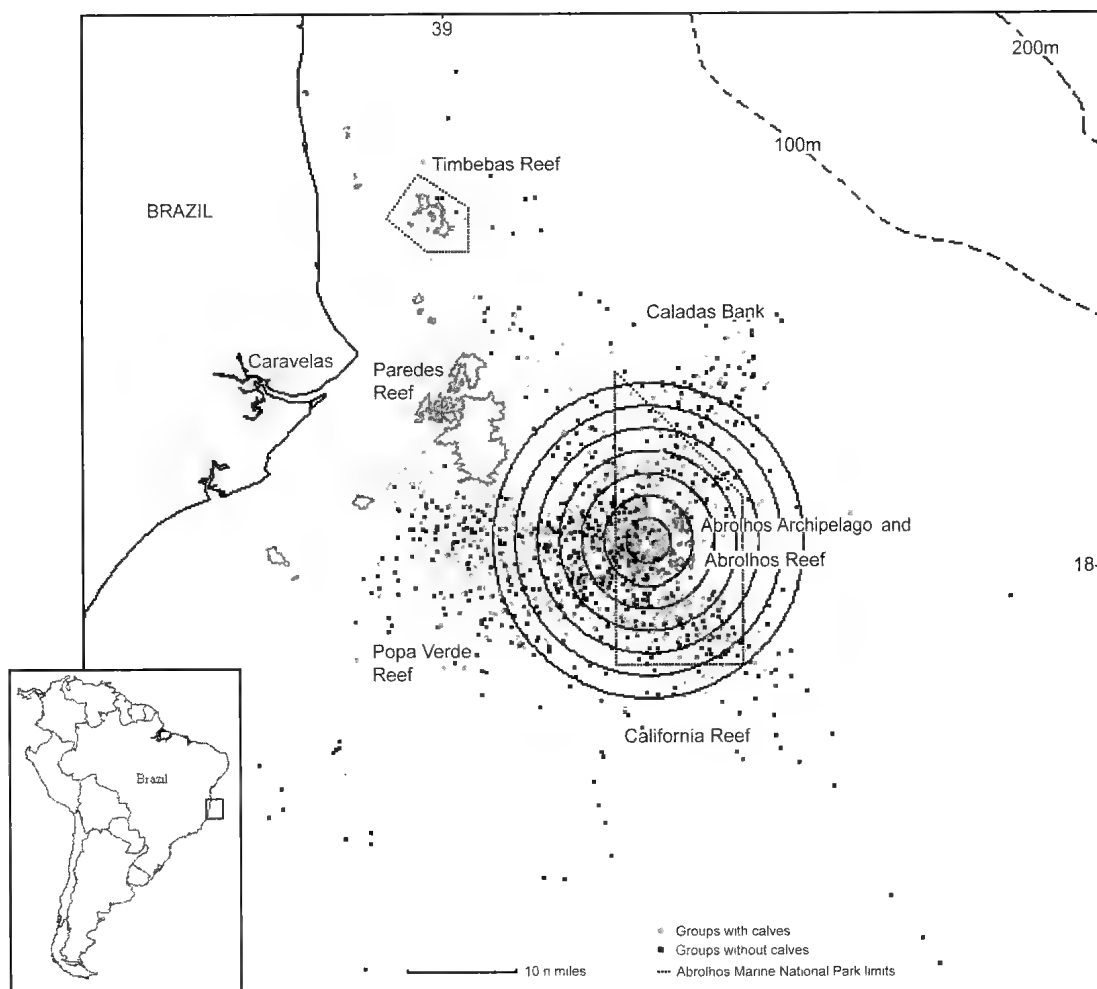


FIG. 1. Distribution map of humpback whale groups sighted in Abrolhos Bank, Brazil, 1992-1998.

collected from 1992-1998, and provides complementary information to the tourism management plan for the Abrolhos region.

#### MATERIAL AND METHODS

**STUDY AREA.** The Abrolhos Bank is located off the northeast coast of Brazil from 16°40'-19°30'S (Fig. 1). It contains a mosaic of coral reefs, mud and calcareous algae bottoms with a mean depth of 30m and covers an area of ~30,000km<sup>2</sup> (Fainstein & Summerhayes, 1982). Five small islands comprise the Abrolhos Archipelago in the north: Santa Bárbara, Redonda, Siriba, Sueste and Guarita. The Brazil Current influences the hydrodynamic conditions of the area. Divergence of the current, due to shallow depths of the bank, cause wind to be an

important component over the continental shelf (Stamo et al., 1990). Generally winds are from the NE from September-February, S from March-August and E from August-September (IBAMA/FUNATURA, 1991). Average annual sea surface temperatures range from 22°-27°C (winter from 22°-24°C) and show a weak vertical gradient. Tide variation is ~2.3m (Castro & Miranda, 1998). The Abrolhos Marine National Park is located in the northeast portion of the bank, and includes the Abrolhos Archipelago and Abrolhos and Timbebas Reefs (Fig. 1).

**DATA COLLECTION.** Data were collected from 1992-1998 between July-November. Survey vessels were trawlers and schooners of lengths between 46-65ft, capable of speeds up to 9 knots, with the 46ft IBAMA trawler 'Benedito' used

most often. Systematic searching for whale groups commenced in 1995 when four-day cruises were conducted each week with searches carried out by a team of three people. Surveys were not conducted when winds were  $>20$  knots. Each daily cruise would head to a pre-specified region on the Abrolhos Bank (i.e. Caladas Bank, Popa Verde Reef, California Reef; Fig. 1). Deviation from track lines occurred when a whale group was sighted. Within a maximum observation time of 30 minutes, photo-ID and biopsies of all animals were attempted, after which the vessel returned to the previous course. Because the main objective of cruises was not for the purpose of the present study, but for photo-ID and biopsies, track lines were sometimes abandoned when large numbers of whales were encountered away from the vessel's planned course.

For each sighting we recorded: date, time, size and composition of group, location (by GPS), behavior, presence of marks or scars and photo-ID and biopsy information. Initial positions of all groups were plotted on nautical charts and water depths interpolated from the chart isobaths.

Bathymetric values of the water column in the region were digitised from local charts (DHN 1300, 1310, 1311) to obtain distribution maps of humpback whales in the study area. A digitising tablet (Calcomp Microgrid IV, A0 format) and Autocad XIV software were used. The graphic Autocad file (DWG format) was exported to DXF format from which the output was saved as a text file. Coordinates and water depth of the digitised points were filtered from this file and processed using SURFER software to create a regular grid with  $0.0025^\circ$  (277.8m) resolution. This was executed using the Kriging routine, with a numeric model of the sea floor. From this file the water depth values corresponding to sighting positions of the data sheet were selected by proximity. A geographical reference search routine was developed using Matlab software.

**ADOPTED TERMINOLOGY.** Solitary animals were termed as single. A group was defined as two or more animals that remained together during the observation period. Generally, members of a group surface and dive synchronously (Clapham, 1993) and maintain the same displacement speed and direction. From Tyack & Whitehead (1983), an escort is a whale that accompanies a female in a competitive group, or that joins a mother-calf pair; principal escort is a whale that remains mostly at a female's side; secondary escort(s) are one or more whales that compete for the position of principal escort;

nuclear individual is a female identified by its centrality and its lack of response to the approach of another adult.

To analyse the habitat use patterns in relation to different group types, we adopted six categories: 1) single – lone individual of unknown sex; 2) pair – two individuals of unknown sex; 3) competitive group (CG) – three or more individuals (sometimes possible to identify a nuclear individual); 4) mother-calf pair (MoCa) – a female with its calf; 5) competitive group with a mother-calf pair (MoCa+CG) – a female and its calf accompanied by a principal escort and one or more secondary escorts; 6) mother-calf-principal escort (MoCaPe) – a female and calf accompanied by a principal escort. Since sub-adults could not be reliably distinguished from adults, all non-calves were considered as adults.

## ANALYSIS

A value of Sightings per Unit of Effort (SPUE) was calculated for 1995-1998 when the systematic survey efforts were similar. SPUE values are expressed as the number of whales sighted per hour of effort for each fortnight during the season. SPUE values may be underestimated because the sampling effort not only represents search time but also includes time spent navigating, observing and collecting data.

All sightings from 1992-1998 containing accurate information on group composition and location were used to analyse the relationship with water depth. The latter was selected as the dependent variable to be tested against group category. Each sighting was treated as an independent sample.

Analysis of Variance was used to determine the effect of group type on mean depth. Once the hypothesis of equal mean depth for all group types was rejected ( $\alpha = 5\%$ ), Tukey's post-hoc test was used to verify which group types had significantly different mean depths.

To analyse the distribution of groups in relation to their distance from islands we defined concentric circular areas with radii varying from 2-14 nautical miles (1 n.m. = 1.852km). Concentric areas were centred on  $17.9666^\circ\text{S}$   $38.70^\circ\text{W}$ , the geographical centre of the Abrolhos Archipelago (Fig. 1). Groups present in each area were divided into two categories: those containing at least one calf and those without calves. A Kolmogorov-Smirnov test (Zar, 1974) was applied to determine if the distribution of these two categories differed relative to distance from the Archipelago centre.

TABLE 1. Summary of survey effort and sighting rates 1992-1998 on Abrolhos Bank, Brazil (SPUE = Sightings Per Unit of Effort).

Year	No. of days	Effort (Hours)	No. of Sightings	SPUE
1992	58	287	199	0.7
1993	48	273.5	290	1.1
1994	58	345.1	458	1.3
1995	59	410.4	592	1.4
1996	68	365.5	701	1.9
1997	75	490.7	871	1.8
1998	72	490.9	799	1.6
Total	438	2663.1	3910	

## RESULTS

Table 1 summarises the observation effort, number of humpback whales sighted and counting rates (SPUE) in the Abrolhos Bank region from 1992-1998. For the systematic surveys during the breeding seasons of 1995-1998, SPUE were highest in the first half of September 1995 and 1997 and in the second half of that month in 1996; in 1998, SPUE peaked in the second half of October (Table 2; Fig. 2).

Temporal trends for group categories are shown in Fig. 3. Singles and pairs were the most frequent groups early in the season. The proportion of competitive groups without calves decreased as the number of competitive groups accompanying a mother-calf pair increased. Singles, pairs, and mother-calf pairs were most frequent during the study period; the latter representing up to 70% of sightings at the end of the season.

To test the relationship between mean depth and group occurrence, the position of 1,437 groups (3,336 whales) were plotted: 226 singles, 418 pairs, 195 competitive groups, 62 competitive groups with mother-calf pair, 331 mother-calf pairs, 205 mother-calf-escorts. Mean group size was 2 and the largest group sighted was 9.

Mean ocean depth for all groups was 17.4m (SD=7.6). An analysis of variance rejected the  $H_0$  hypothesis of equal distribution of the groups, independent of depth ( $F = 13.9$ ,  $p = 0.05$ ). Groups comprising mother-calf pairs and mother-calf-escort were found in shallower waters than other groups (Table 3; Fig. 4). Competitive groups with mother-calf pairs were found in waters with a mean depth of 16.4m (SD=7), showing no significant difference to other categories. Groups without calves were found in deeper waters than groups with calves (Table 3; Fig. 4).

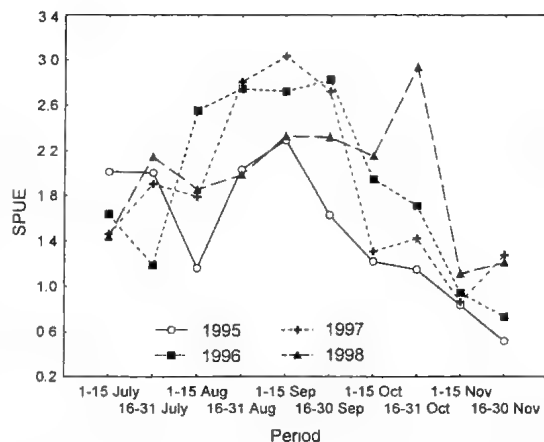


FIG. 2. Sightings per unit of effort for each fortnight from July 1 to November 30, 1995-1998.

Groups with calves occurred in higher proportions <4 nautical miles from the archipelago ( $D = 0.139$ ;  $\chi^2 = 18.516$ ;  $p < 0.05$ ) (Table 4). The ratio between groups with and without calves progressively decreases beyond 4 nautical miles (Fig. 5). Within 14 nautical miles of the archipelago centre, 440 groups with calves and 526 groups without calves were sighted. Outside this area, 158 groups with calves and 313 groups without calves were sighted.

## DISCUSSION

Sighting rates (SPUE) are high in July compared with those at the end of the season, suggesting that whales arrive in the breeding ground before surveys began. Anecdotal

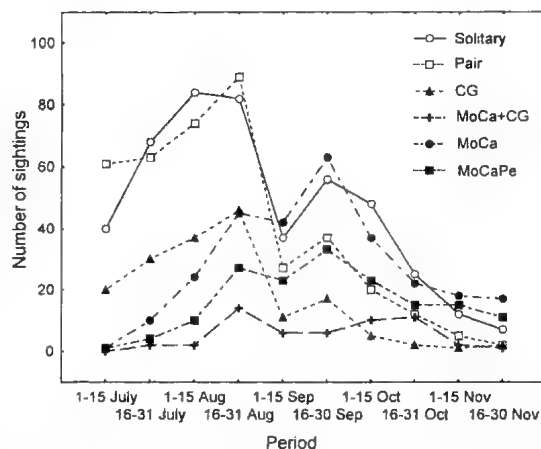


FIG. 3. Number of sightings per group categories for each fortnight from July 1 to November 30, 1995-1998.

TABLE 2. Sightings per unit of effort (SPUE) for each fortnight during the humpback whale breeding seasons, 1995-1998 (n = number of whales sighted, E = sample effort in hours).

Period	1995			1996			1997			1998		
	n	E	SPUE	n	E	SPUE	n	E	SPUE	n	E	SPUE
1 to 15 July	31	15.4	2	35	21.3	1.6	83	56.6	1.4	72	50	1.4
16 to 31 July	78	38.9	2	44	37	1.2	74	38.9	1.9	91	42.4	2.1
1 to 15 August	44	37.8	1.1	106	41.5	2.5	118	66	1.8	127	68.6	1.8
16 to 31 August	142	69.75	2	153	55.6	2.7	177	63	2.8	211	106.3	2
1 to 15 September	60	26	2.3	71	26.1	2.7	89	29.3	3	62	26.6	2.3
16 to 30 September	108	66.3	1.6	121	42.75	2.8	127	46.7	2.7	54	23.25	2.3
1 to 15 October	36	29.5	1.2	43	22.1	1.9	89	68	1.3	121	56.1	2.1
16 to 31 October	59	51.3	1.1	72	42.1	1.7	36	25.25	1.4	24	8.16	2.9
1 to 15 November	30	36.1	0.8	34	36.1	0.9	25	29.1	0.8	25	22.5	1.1
16 to 30 November	4	7.75	0.5	22	30.1	0.7	53	41.5	1.3	12	9.9	1.2
Total	592			701			871			799		

information corroborates this. According to fishermen and tourist vessel skippers many whales are seen in the area in June and one sighting has been recorded in mid May (R.C. Fortes, pers. comm.). Researchers assessing the standing stock in the Brazilian Economic Exclusive Zone (EEZ) also reported the presence of humpback whales near Abrolhos in May (A.B. Greig, pers. comm.).

The highest SPUE of the study period was for the first half of September 1997 (3 whales/hour) (Fig. 2). Time of abundance peak varied little between years. The most atypical was 1998 with peak concentration in the second half of October; a shift of six weeks compared with 1995 and 1997, and four weeks compared with 1996. In this period only one cruise was undertaken, due to poor weather, with high sightings recorded. In September of the same year, a cruise was made north of the Abrolhos Bank to the Porto Seguro region, an area not normally sampled. The SPUE recorded in this area varied between 0.009-0.03

individuals/hr. During the same month, at the Abrolhos Bank area, SPUE varied from 0.025-0.07 ind/hr. This diversion from the main area of humpback whale concentration may have contributed to the decrease in SPUE for September 1998. Changes of three and four weeks in the peak of the breeding season were observed for humpback whales in Hawaii (Baker & Herman, 1981) and of about two weeks for gray whales, *Eschrichtius robustus*, in Laguna Saint Ignacio, California (Jones & Swartz, 1984).

The majority of humpback whale sightings were in the north around the Abrolhos Archipelago. Most survey effort was concentrated in this area and could have biased the results. In areas of low survey effort, where fewer whale numbers were expected (e.g. Porto Seguro), low SPUE values supported the hypothesis that the Archipelago is a concentration area. Nevertheless, in recent years sightings have increased further north on the Abrolhos Bank (Zerbini et al., 2000) to the Fernando de Noronha Archipelago (3°51'S 32°25'W)

TABLE 3. Tuckey test for the depth variable against group categories: single; pair; competitive group (CG); competitive group with mother-calf pair (MoCa+CG); mother-calf pair (MoCa); mother-calf-principal escort (MoCaPe). (M = mean depth for each group category; SD = standard deviation; \* significant difference [ $p < 0.05$ ] between the categories).

Groups	Single	Pair	CG	MoCa+CG	MoCa	MoCaPe
	M=18.9 (SD=7.6)	M=18.6 (SD=7.9)	M=19.1 (SD=8)	M=16.4 (SD=7)	M=15.8 (SD=6.8)	M=14.9 (SD=7)
Single		0.993	0.999	0.184	0.00004*	0.00002*
Pair	0.993		0.958	0.287	0.00003*	0.00002*
CG	0.999	0.958		0.134	0.00003*	0.00002*
MoCa+CG	0.184	0.287	0.134		0.991	0.697
MoCa	0.00004*	0.00003*	0.00003*	0.991		0.714
MoCaPe	0.00002*	0.00002*	0.00002*	0.697	0.714	



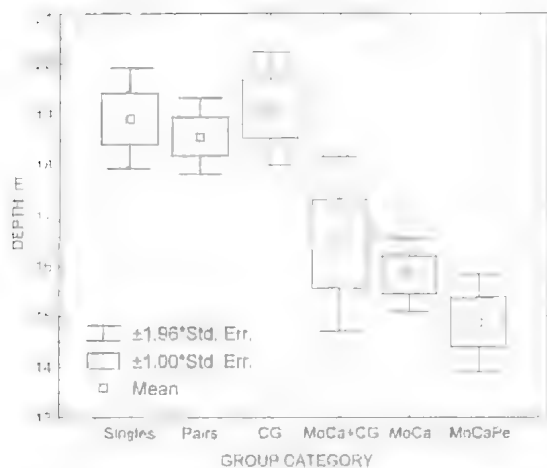


FIG. 4. Mean water depth for each group category: single; pair; competitive group (CG); competitive group with mother-calf pair (MoCa-CG); mother-calf pair (MoCa); mother-calf-principal escort (MoCaPe).

(J.M. Silva Jr. pers. comm.). This may indicate that the species is returning to areas previously occupied before the depletion of stocks by whaling.

**GROUP CATEGORIES.** Single whales and pairs were the most frequent groups at the beginning of the season (Fig. 3). The proportion of singles decreased from August and that of mother-calf pairs increased. Formation of competitive groups was observed throughout the season. Competitive groups with a mother-calf pair were fewer than other categories. Clapham et al. (1992) noted a similar pattern in the West Indies.

**WATER DEPTH.** Distribution of groups was strongly related to water depth. Highest mean depths were noted for competitive groups, but there were no significant differences between

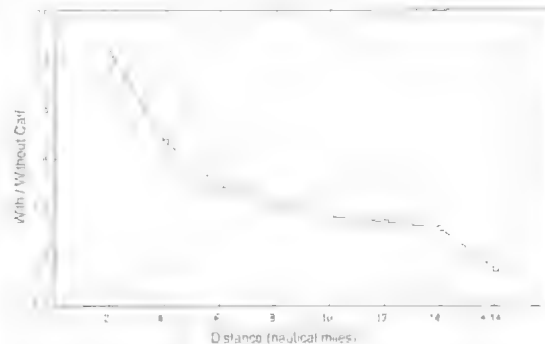


FIG. 5. Ratio of number of groups with calves to those without calves within distances show from the centre of the Abrolhos Archipelago, 17.966°S 38.7°W.

singles, pairs and competitive groups. All groups with calves were in shallower waters, although there was no significant difference between competitive groups with cow-calf pair and all other categories.

Distribution of mother-calf groups may be influenced by water dynamics. Within 4nm of the Archipelago centre, groups with calves were in higher proportions than groups without calves. A shore based study from an archipelago island (Projeto Baleia Jubarte/IBAMA, 1998) recorded that 49.3% of groups contained a calf in 1997 and 46.9% in 1998, inside a 4nm area from the Abrolhos Archipelago centre; higher percentages than for this study. However, that study site is characterised by the shallowest waters of the Abrolhos Bank (Fig. 1), comprising the Abrolhos Archipelago and the Abrolhos Reef which offer protection from prevailing winds and attenuation of the dynamics of water movement. Such calm water may assist calf suckling, potentially allowing the calf to remain next to the mother with less effort. Studies at Hawaiian and Caribbean wintering grounds demonstrated segregation according to sex, age and/or reproductive status, with humpback whale cows with calf appearing to predominate in shallow, sheltered or coastal water, while other adults were mostly in deeper, more exposed water (Hermam & Antinaja, 1977; Whitehead & Moore, 1982; Mattila & Clapham, 1989; Glockner-Ferrari & Ferrari, 1990; Smultea, 1994).

Disposition of cow-calf pairs towards shallower waters may be a strategy to avoid interactions with competitive groups where behavior within such groups might be harmful to a calf. Cartwright (1999) noted that calf behavior was energetically conservative when alone with its mother, but

TABLE 4. Kolmogorov-Smirnov test for two samples. Groups with (y) and without (n) calves as a proportion of the total in each category, recorded within the distances show from position 17.966°S 38.7°W, the center of the Abrolhos Archipelago.

Distance (n. miles)	Groups with calves (y)	Groups without calves (n)	D(y)-D(n)
2	0.143	0.053	0.090
4	0.302	0.163	0.139
6	0.443	0.316	0.127
8	0.654	0.517	0.128
10	0.786	0.707	0.079
12	0.886	0.835	0.051
14	1	1	1

became more costly when associated with multiple escorts. In most cases an escort is male (Baker & Herman, 1984), and generally believed to be mature, awaiting an opportunity to copulate with the mother when she comes into oestrus (Clapham et al., 1992). Mother-calf pairs with a principal escort were associated with shallowest waters (Table 3). Behavior of mother-calf-escort groups in frequenting shallow waters may be a strategy of the cow to avoid mating. Jones & Swartz (1984) suggested that competitive groups select deeper waters to avoid collisions with the seabed and coral heads and that shallow waters may discourage courting males.

Payne (1986) studied southern right whales, *Eubalaena australis*, in the Valdes Peninsula, Argentina and observed that cow-calf pairs were distributed along the coast, following the 5m isobath. That author identified three areas occupied by different group categories: one predominantly occupied by mother-calf pairs; one with mature males and females; and one with all the classes including sub-adults and competitive groups. Glockner-Ferrari & Ferrari (1985, 1990) and Salden (1988) recorded a continuous decrease in the cow-calf pair percentage in Hawaiian coastal waters, and associated this with the increase of human activities in the area. However, the Hawaiian population continued to increase (Bauer et al., 1993).

It is important to determine the habitat use patterns of humpback whales in their breeding grounds before the introduction of activities that may alter this pattern (Smultea, 1994). Whale watching activity in the Abrolhos Bank area is opportunistic and most whale groups are observed in tracks of boats proceeding to the Abrolhos Marine National Park (Fig. 1). An agreement in 1999 between the Abrolhos Marine National Park and the Projeto Baleia Jubarte noted that boats would not approach whale groups inside the archipelago area. A shore based study of the impact of whale watching activity on whale behaviour began in 1997. Continuous monitoring of habitat use patterns in the Abrolhos Bank area, with special reference to the Abrolhos Archipelago, could detect possible trends and assist in management of this activity, based on Federal Edict no. 117/96. Aerial surveys are suggested to determine humpback whale population distribution and to monitor possible trends. Such data would contribute to a better understanding of habitat selection by different group types, provide abundance estimates for comparison with data obtained from mark-recapture models of photo-identified whales, and provide essential

information for management of whale watching operations in the area.

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ENCOUNTER RATES OF WHALES AROUND THE ANTARCTIC PENINSULA WITH  
SPECIAL REFERENCE TO HUMPBACK WHALES, *MEGAPTERA NOVAEANGLIAE*, IN  
THE GERLACHE STRAIT: 1997/98 TO 1999/2000

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During the austral summers of 1997/98 to 1999/00, the Projeto Baleias/Brazilian Antarctic Programme conducted ship-based surveys of cetacean distribution and sighting frequencies in the Gerlache Strait and around the South Shetland Islands - Antarctic Peninsula region. These surveys included humpback whales (*Megaptera novaeangliae*), for which biopsy sampling and photo-identification were also undertaken. Data gathered during the 1997/98 summer season indicate that the humpback whale is the most commonly seen cetacean in the surveyed areas. Its high encounter rate (0.32 whale/nautical mile) was followed by minke whales, *Balaenoptera* spp. (0.14 whale/nautical mile), killer whale, *Orcinus orca* (0.03 whale/nautical mile), sei whale, *B. borealis* (0.01 whale/nautical mile) and other unidentified animals (0.004 whale/nautical mile). The highest encounter rate for humpback whales was in the Gerlache Strait (0.42 whale/nautical mile; CV = 55.5%), where encounter rates were obtained from six surveys (1997/98), three surveys (98/99) and two surveys (99/00), allowing for inter-annual comparisons. Although a decrease in the mean encounter rate of humpback whales in the Gerlache Strait was observed over the period, Anova and Kruskal-Wallis tests showed no statistical significance. A longer time series would be necessary to draw conclusions with respect to temporal trends. □ *Humpback whale, cetaceans, population density, Antarctic Peninsula, Gerlache Strait.*

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Historic and current information on the abundance of southern humpback whales, *Megaptera novaeangliae*, is scarce, though catch data suggest that the species was abundant prior to the modern whaling era (Gambell, 1973a; Mizroch, 1984). During the 20th century, humpback whales were extensively hunted in the Southern Hemisphere (Tønnessen & Johnsen, 1982). High catch rates reduced the population to only a few percent of its estimated original size (e.g. Gambell, 1973b, 1974; Breiwick & Braham, 1984; Mizroch, 1984). However, some population data were gathered during this period (e.g. Mackintosh, 1942; 1965; 1972; Dawbin, 1964;

1966; Chittleborough, 1965), whereas information after the cessation of commercial whaling is sparse. The necessity to comprehensively assess the current status of humpback whales in the Southern Hemisphere has led the International Whaling Commission (IWC) to recommend multilateral studies in the species' breeding and feeding grounds. Several cruises have been conducted in the Southern Ocean (e.g. IWC/IDCR, Japanese scouting vessel surveys), but it remains important that any surveys conducted in this area include a cetacean component. In the 1994/95 austral summer we participated in the Brazilian Antarctic Programme (PROANTAR), created in

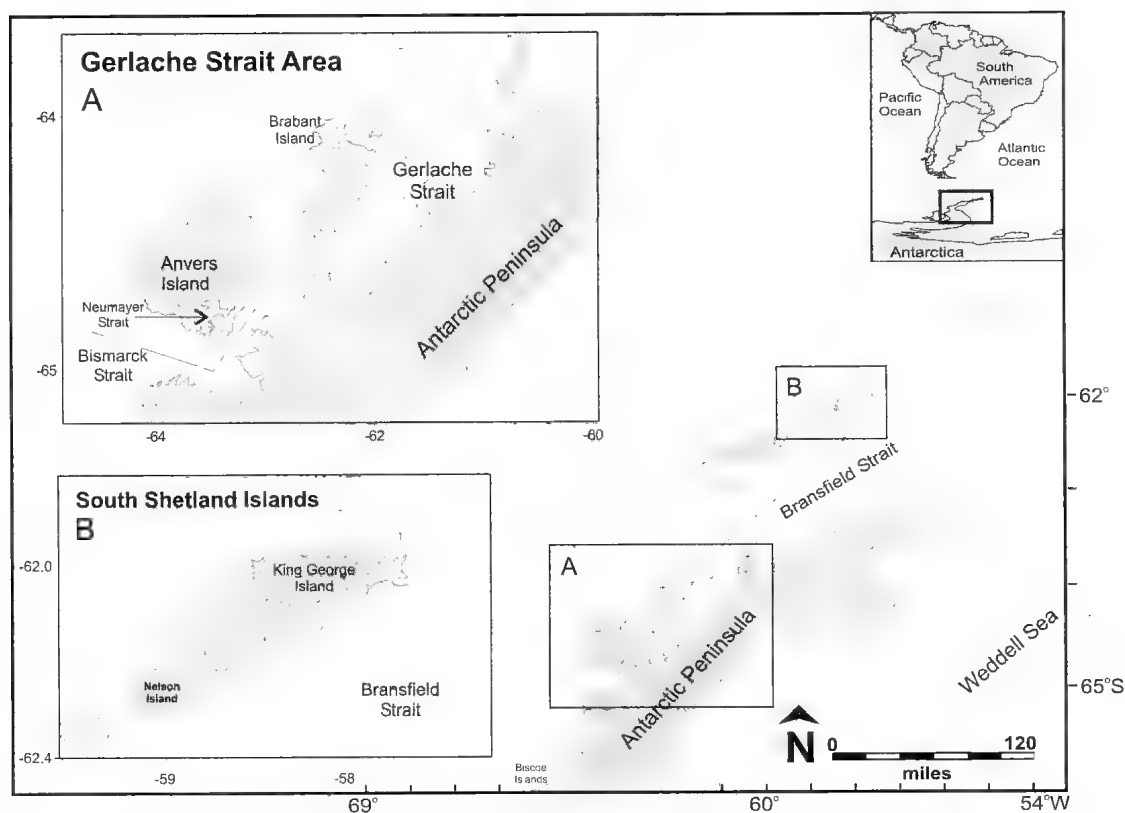


FIG. 1. Study area around Antarctic Peninsula. Transect lines for each surveyed region are shown in detail.

1982 within the aims and policies of the Antarctic Treaty. During the first year of the cetacean component within PROANTAR (herein referred as Projeto Baleias/PROANTAR), we evaluated the suitability of using a ship as a platform of opportunity to study cetaceans in the Antarctic. Our major objective was defined as providing information to improve assessment of humpback whales in the Southern Hemisphere (Secchi et al., 1999). In the summer of 1997/98 we began to: 1) photo-identify humpback whales around the South Shetland Islands and the Antarctic Peninsula (for comparison with international catalogues); 2) biopsy humpback whales from the same areas for DNA and pollution analyses; 3) estimate cetacean encounter rates in these areas; and 4) record all cetacean sightings.

This paper compares the encounter rates of humpback whales in the Gerlache Strait in the summers of 1997/98 to 1999/2000. For 1997/98 we also compared the encounter rates of humpback whales with other areas around the South Shetland Islands and with those of other cetaceans.

## MATERIAL AND METHODS

During the austral summers of 1997/98 to 1999/2000, the Projeto Baleias/PROANTAR conducted ship surveys to determine cetacean distribution and encounter rate estimates in the Gerlache Strait and around the South Shetland Islands - Antarctic Peninsula region (the boundary between IWC management areas I and II; see Donovan, 1991) (Fig. 1). Special attention was paid to photo-identification (see Dalla Rosa et al., 2001) and biopsy sampling of humpback whales. Surveys were conducted onboard the 75m Oceanographic and Supply Vessel (NApOc) 'Ary Rongel'. Although most survey transects were conditioned to the navigation schedule of Projeto Baleias/PROANTAR, dedicated cetacean surveys were performed in the Gerlache Strait. In this area, whale encounter rates were obtained from six (1997/98), three (98/99) and two transects (99/00), allowing for inter-annual comparisons. For each intra-annual survey the mean encounter rate and its respective variation was estimated using each transect as a sample. Sighting per unit of effort (SPUE), as the rate of

sighted whales per nautical mile surveyed, was used as a simple index of density. Since it is known that the detection probability varies among species (Kasamatsu et al., 1996), the encounter rates of different species were not directly compared in the statistical analysis. For the 1997/98 summer, encounter rates were compared between several surveyed areas.

Observation platforms were the exterior wings of the bridge, ~14m above sea level, except during unfavourable weather conditions (sea state above Beaufort 4, low visibility) when the observers used the bridge. A full search for cetaceans was conducted whenever the vessel was under way and weather was favourable. The number of observers varied from one to three (mostly two), who generally rotated every 30 minutes at each wing of the ship. Each person worked for 90 minutes and rested for 30 minutes. Each observer covered one side of the vessel's trackline forward of the beam (90° quadrant). Three observers were used only when one observer had no previous experience. In such cases the data recorder helped the least experienced observer. Data collected for each sighting included: species (minke whales were not distinguished to form), number of whales, miles navigated, position, date, time and weather and sea condition. Ship speed varied from 10-12 knots, depending on the number of growlers and icebergs in the vicinity. Most surveys followed a 'passing mode' method with the exception being the 1997/98 survey in the Gerlache Strait, which followed a 'closing mode' on occasions when photo-identification was conducted simultaneously. In these cases one observer stayed on the bridge to record any whales passed by the ship. Whales were searched for using the naked eye and 7x50 binoculars. Binoculars were also used to identify species and numbers of individuals. Only data obtained during searching effort were considered in the analysis (i.e. crew and researcher sightings made 'off effort' were not included). Search effort was restricted to sea conditions ranging from Beaufort scale 0-4 (mostly <3) to reduce effects on sighting probability. We consider that this variable did not strongly influence encounter rate estimates. Visibility was generally sufficient to allow reliable sightings in terms of species identification and estimation of group size up to a distance of two nautical miles (for large whales). Although visibility categories tend to be subjective (as Beaufort sometimes is) and may vary among observers, its final classification was defined on a common sense basis. Completely

clearsky was considered as an excellent visibility condition. When fog slightly limited observer's sight of the horizon, visibility was classified as moderate. An approximate control of the observer's limit of visibility was obtained by using the ship's radar to read distances from the ship to growlers and icebergs.

Anova and Kruskal-Wallis tests were applied to test for differences between humpback whale encounter rates in the Gerlache Strait for the three periods.

## RESULTS

**WHALE ENCOUNTER RATES AROUND THE ANTARCTIC PENINSULA.** Whale encounter rates for the summer of 1997/98 were highest in the Gerlache and Bransfield Straits (0.62 whale/nm) and lowest around King George Island (0.19 whale/nm) (Table 1). Estimated mean encounter rates showed humpback whale to be the most commonly seen species in the surveyed areas (0.32 whale/nautical mile), followed by minke whales, *Balaenoptera acutorostrata* + *B. bonaerensis* (0.14 whale/nautical mile), killer whales, *Orcinus orca* (0.03 whale/nautical mile), sei whales, *B. borealis* (0.01 whale/nautical mile), and other unidentified animals (0.004 whale/nautical mile). The few sightings of southern right whales, *Eubalaena australis*, and fin whales, *B. physalus*, occurred outside the surveyed areas or during off-effort times. Our results show a high concentration of humpback whales in protected coastal waters to the west of the Antarctic Peninsula, making them the most frequently sighted species in the area. This agrees with the long-term serial data presented by Kasamatsu et al., (1996), which also indicated the highest encounter rate of humpback whales to be west of the Antarctic Peninsula, between 60°W and 80°W. These authors found the latitudinal peak in encounter rates to be between 62°S and 66°S, which also matches our findings. The northern and southern boundaries of the Gerlache Strait (ca. 63°45'S to 65°00'S), the area where we recorded the highest encounter rates for humpback whales, are within those limits. This is intermediate to the latitudinal peaks for blue whales, which are found further south ( $\geq 66^\circ\text{S}$ ), and fin whales, found further north ( $\leq 58^\circ\text{S}$ ) (Kasamatsu et al., 1996).

Minke whales produced the second highest encounter rate (0.14 whale/nautical mile; CV = 122.7%) in the region. A high coefficient of variation (calculated from the density values recorded for all surveyed areas) is attributed to

TABLE 1. Summarised whale densities around the Antarctic Peninsula during the Brazilian Antarctic Survey XVI (summer 1997/98).

Area	Species	No. of whales	N miles surveyed	Sighting frequency
Gerlache Strait	humpback	153	312.2	0.49
	minke	16		0.05
	killer	24		0.08
	Total	193		0.62
King George Island	humpback	26	146.5	0.18
	minke	1		0.01
	Total	27		0.19
Bismarck Strait	humpback	13	33.4	0.39
	minke	2		0.06
	Total	15		0.45
Neumayer Passage	humpback	0	19.0	0
	minke	6		0.32
	Total	6		0.32
Biscoe Islands	humpback	9	26.5	0.34
	minke	0		0
	unidentified	1		0.04
	Total	10		0.38
Bransfield Strait	humpback	48	229.8	0.21
	minke	86		0.37
	sei	6		0.03
	unidentified	2		0.01
	Total	142		0.62
General	humpback	249	767.4	0.32
	minke	111		0.14
	sei	6		0.01
	killer	24		0.03
	unidentified	3		0.004
	Total	393		0.51
Average and (C.V.)	humpback			0.27 (65.1%)
	minke			0.14 (122.2%)
	Total			0.43 (39.5%)

the aggregative behaviour of the species. Single minke whales have been observed in some areas (e.g. Neumayer and Gerlache Straits) whilst groups of tens of individuals were seen in others (e.g. Bransfield Strait). Although it is not recommended to make direct comparisons of encounter rates of different species, because the search half-width varies between species (mostly when they are different in size and behaviour, Kasamatsu et al., 1996), in some areas encounter rates were higher for minke whales than for humpback whales (e.g. Neumayer and Bransfield

Straits). Considering that minke whales have a much lower value of search half-width than humpback whales (see Kasamatsu et al., 1996) it is suggested that the former have a much higher relative density in those areas. A high sighting frequency for minke whales was also observed on the eastern side of the Antarctic Peninsula, where humpback whales were uncommon (Projeto Baleias/PROANTAR, unpubl. data). In the Gerlache and Bismarck Straits and near the Biscoe and King George Islands, minke whales were comparatively rare while humpback whales presented high encounter rates. The Gerlache and Bismarck Straits are adjacent to areas of high minke whale encounter rates, leading us to hypothesise that the two species may avoid ecological competition in the area, but further investigation is recommended. Latitudinal habitat segregation (or separation) between some baleen whales and toothed whales in the Antarctic has been suggested as an evolving adaptation to reduce competition for food (Kasamatsu & Joyce, 1995; Kasamatsu et al., 1996).

Sighting frequency of sei whales was low in the study area. Most sighting records during the Projeto Baleias/PROANTAR surveys occurred in the Drake Passage, north of the Antarctic Peninsula (Dalla Rosa et al., 1996; Projeto Baleias/PROANTAR, unpubl. data). Kasamatsu et al. (1996) also found that sei whale distribution was more restricted than that of other species and that the distribution in the Southern Ocean seems to be limited to warmer northern Antarctic waters (see also Kasamatsu et al., 1988). Mackintosh (1965) suggested that sei whales prefer warmer waters than fin and blue whales.

The lack of sightings of fin whales in sheltered areas around the Antarctic Peninsula conforms with previous studies. During the IWC/IDCR cruises from 1978/79 to 1983/84 nearly 70% of the sightings of this species were made in waters > 60 miles from the pack ice, with relatively large concentrations around the coordinates 58°S and 58°W, in the Drake Passage (see Kasamatsu et al., 1988). Kasamatsu et al. (1996) report a high concentration of fin whales between 40°W and 60°W and 54°S and 58°S. The species has frequently been observed within these coordinates when the Brazilian ship sailed from the South Shetlands to Elephant Island and from the latter to South America (Projeto Baleias/PROANTAR, unpubl. data). Armstrong et al. (1998) witnessed several groups feeding ~35 miles NE of Elephant Island (ca. 60°46'S 55°25'W) in February, 1997. These records suggest that the waters around



TABLE 2. Cetacean encounter rates (animals/nautical mile surveyed) in the Gerlache Strait (ca. 63°44'S 61°07'W to 64°59'S 63°23'W), Antarctic Peninsula.

	No. of cetaceans	Humpback	Minke	Killer	Miles surveyed	Beaufort	Observers	Visibility	Date	Humpback Enc. rate	Minke Enc. rate	Killer Enc. rate
1997/98												
Sample 1	16	15	0	0	51	1	1 to 3	good	25/01/98	0.29	0	0
Sample 2	19	19	0	0	21.5	1 to 3	3	good	27/01/98	0.88	0	0
Sample 3	45	42	0	0	69	1	3	good	03/02/98	0.61	0	0
Sample 4	29	28	1	0	74	1 to 4	3	moderate	04/02/98	0.38	0.014	0
Sample 5	26	11	9	6	38.1	3	3	good	07/03/98	0.29	0.24	0.16
Sample 6	59	38	3	18	58.6	1 to 3	2 to 3	good	08/03/98	0.65	0.05	0.31
Average (CV%)										0.52 (46%)	0.05 (54%)	0.08 (60%)
1998/99												
Sample 1	61	31	9	18	58.8	1 to 2	2	good/moderate	27/01/99	0.53	0.15	0.31
Sample 2	10	8	2	0	29.7	1	2	good	29/01/99	0.27	0.07	0
Sample 3	44	26	17	0	66.5	0 to 1	2	excellent	01/02/99	0.39	0.25	0
Average (CV%)										0.40 (33%)	0.16 (58%)	0.10 (173%)
1999/00												
Sample 1	31	6	8	17	91.8	2	2	good	13/12/99	0.07	0.09	0.19
Sample 2	54	18	19	11	82.6	1 to 2	2	good	9/01/00	0.22	0.23	0.13
Average (CV%)										0.15 (73%)	0.16 (62%)	0.16 (27%)

Elephant Island are important concentration areas for fin whales.

The absence of blue whales in the survey area also conforms with previous studies. Kasamatsu et al. (1996) demonstrated a gap in the distribution of blue whales between 40°W and 60°W in the South Atlantic sector of the Antarctic (see also Kato et al., 1995).

**INTER-ANNUAL COMPARISONS OF HUMPBACK WHALE DENSITIES IN THE GERLACHE STRAIT.** Effort and whale encounter rates in the Gerlache Strait during the 1997/98 to 1999/2000 austral summers are presented in Table 2. Humpback whales presented a high encounter rate (mean estimated for the three surveys = 0.42 whale/nm; CV = 55.5%). This is about twice the estimates reported by Stone & Hamner (1988) for the same area. This difference may have arisen from temporal variation both within and between years in the humpback whale density in this area. Within-season differences in density may be related to timing of migration (see Fig. 2 and related discussion). Our surveys covered the area from early December to early March, with most of the effort concentrated in

January and February while Stone & Hamner (1988) surveyed from 2 to 20 April, near the end of the feeding season. However, inter-annual variation may also explain the difference in density between the two studies in the Gerlache Strait, and may be related to temporal changes in prey density.

The apparent decrease in mean encounter rate of humpback whales observed over the three years (see Table 2) is not statistically significant [Anova:  $F(2.8) = 2.41$ ;  $p = 0.085$  and Kruskal-Wallis  $H(2, N=11) = 4.93$ ;  $p = 0.151$ ]. A previous comparison between the first two periods, using t-statistics (Montgomery, 1984) through a randomisation test (Good, 1994), also displayed no statistical significance (Dalla Rosa et al., 1999). It would be reasonable to suppose that variation in the availability of prey (i.e. krill, *Euphausia superba*) could influence encounter rates of humpback whales. A gradual decrease in food availability may force whales to move to other areas. According to Brieley et al. (1999) and Hewitt & Demer (in press), the krill biomass around Elephant Island oscillates, varying from high to low within periods of about three to four

years. We suggest that the expected biomass should have reached low levels in summer 1999/2000 after a gradual decrease from the previous seasons. While these estimates are for the Elephant Island area, it is believed that these krill densities are representative of those throughout a much larger area of the Antarctic Peninsula region (Roger Hewitt, pers. comm.) (see Siegel & Loeb, 1995; Brieley et al., 1999 for supporting arguments). We could therefore expect a low encounter rate in this area for 1999/2000. However, our data showed a non-significant difference between study years. This suggests that models predicting oscillations in krill biomass may not be useful for predicting trends in whale densities, at least on a short-term basis. Obtaining more data through medium to long-term surveys in this area would enable monitoring of temporal trends in humpback whale densities. Simultaneous studies correlating these trends with environmental variables and krill biomass may elucidate inter-annual changes in humpback whale encounter rates.

**MONTHLY VARIATION OF HUMPBACK WHALE DENSITY IN THE GERLACHE STRAIT.** Encounter rates of humpback whales in the Gerlache Strait by half-month period (Fig. 2) are a combination of values obtained from different years and expeditions (since no significant difference was found in the inter-annual comparisons of humpback whale density estimates). The trend indicates a peak in density from late January to early March. This differs slightly from the results presented by Kasamatsu et al. (1996) who combined data from the entire Antarctic region. Those authors found a peak in humpback whale encounter rates in early January with a steady decrease through February and attributed this pattern to the segregation in the migration of populations described by Dawbin (1966). This variation might be attributed to different spatial and temporal scales between the sources of data. However, the high encounter rate for March and the relatively high encounter rate found in April by Stone & Hamner (1988) suggest that humpback whales remain in the Gerlache Strait as long as mid autumn. We attribute this relatively high density during autumn to the favourable conditions that the species may encounter in the Gerlache Strait; a narrow corridor, between Brabant and Anvers Islands and the Antarctic Peninsula, possibly providing both shelter and abundant krill. Zooplankton samples collected around the Antarctic Peninsula resulted in highest krill densities in the Gerlache

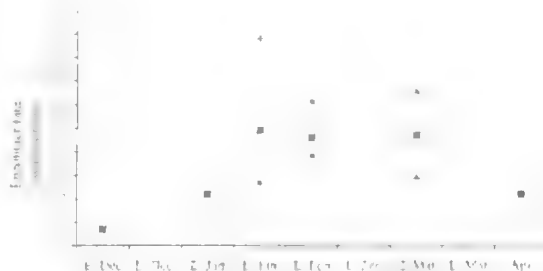


FIG. 2. Seasonal change in the encounter rates of humpback whales in the Gerlache Strait - Antarctic Peninsula, by half-month period from early December to April. Rates are averages from pooled data obtained in the three surveys. Dots represent maximum and minimum values for the period. The value for April taken from Stone & Hamner (1988). (E = early and L = late).

and Bransfield Straits (5717 ind/1000m<sup>3</sup> and 5723 ind/1000m<sup>3</sup>, respectively). Montú et al. (1994) reported decreased concentrations of krill from about 830 ind/1000m<sup>3</sup> to 16 ind/1000m<sup>3</sup> as the distance from those areas increased. High concentrations of phytoplankton are also commonly observed in the area (El-Sayed, 1968; Montú et al., 1995). Loescher et al. (1997) and Bathmann et al. (1997) mention the occurrence of a seasonal input of nutrients and minerals (e.g. Fe) which coincides with blooms of phytoplankton observed in the spring. The oceanographic conditions together with local productivity of phyto and zooplankton may also explain the relatively high densities of humpback whales observed in the Gerlache Strait.

## CONCLUSION

High densities of cetaceans (mainly humpback whales) have been observed in the Gerlache Strait. The area is a narrow corridor (~5-8 miles wide) with relatively calm waters, facilitating reliable observation. Such factors make it a strategic area for further integrated surveys. It may also be useful as a reference for comparing results obtained from ecological studies with the surroundings. Medium to long-term surveys in the area would allow temporal trends in whale densities to be monitored. Trends in whale density and distribution could be evaluated according to the density and distribution patterns of their prey (e.g. years of low krill biomass would be interesting to investigate if predators move to other areas or feed on different prey). Given the high concentration and accessibility of humpback whales in the Gerlache Strait, we

consider the area also appropriate for conducting long term photo-identification and genetic studies, potentially providing important information on site fidelity and migration, and genetic variability both within/between years and within/between areas. Such multidisciplinary studies would provide a valuable contribution to our knowledge of the ecology of the humpback whale in the Antarctic.

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# STATUS OF HUMPBACK WHALES, *MEGAPTERA NOVAEANGLIAE*, IN EAST AUSTRALIA AT THE END OF THE 20TH CENTURY

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The humpback whale stock that migrates along the east Australian coast comprises part of the Area V (130°E–170°W) stock and was monitored by shore-based observations from Point Lookout (27°26'S, 153°33'E) during 1978-1999. Devastated by whaling which ceased in 1962, the stock is estimated to be recovering at a rate of 10.9% per annum (99% CI  $\pm$  1%) and to number 3,600  $\pm$  440 in 1999. Advantages and limitations of the Point Lookout observation methods are discussed. □ *Humpback whale, Megaptera novaeangliae, eastern Australia, stock size, recovery.*

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Dawbin (1966, 1997) reviewed 20th century knowledge of humpback whale migration in the context of whaling operations. He emphasised that, in the Southern Hemisphere, a large proportion of whales travelled near continental shores while migrating between temperate winter breeding grounds and Antarctic summer feeding grounds. Chittleborough (1965) detailed the catch of 7,423 humpback whales during 1952-62 from east Australian shore stations at Byron Bay (28°37'S, 153°38'E) and Tangalooma (27°11'S, 153°23'E). He noted that most were captured <15km from shore and that no alteration in migration patterns was evident at the end of that decade of over exploitation.

Shore-based observations have been used to assess population trends in several baleen whale species. Pre-eminent are those at Monterey of the Californian gray whale, *Eschrichtius robustus*, (see Reilly, 1992). Bowhead whale, *Balaena mysticetus*, surveys were conducted on fast ice at Point Barrow, Alaska from 1978-88 (Krogman et al., 1989; Zeh et al., 1991) and humpback whales were surveyed from Cape Vidal, Natal from 1988-91 (Findlay & Best, 1996a, 1996b).

Since the late 1970s observations from elevated shore positions at Point Lookout (27°26'S, 153°33'E) on North Stradbroke Island have been conducted to assess the status of the east Australian portion of the Area V (130°E-170°W) humpback whale stock (Bryden, 1985; Bryden et al., 1990; Paterson & Paterson, 1984, 1989; Paterson et al., 1994). Those authors assumed that humpback whale migration patterns had not altered in the post-whaling period and Bryden (1985), on the basis of aerial

observations from the shore to 60km seaward in the early 1980s, considered that <5% of north-bound humpback whales passed Point Lookout >10km from shore. This study describes the results of further observations in 1994, 1996, 1998 and 1999 and compares the data with those from our previous surveys.

## POINT LOOKOUT OBSERVATIONS

The methods conformed with surveys dating from 1978, described by Paterson et al. (1994). All observations from 1978-99 were made by RP and PP from the same 67m high position. In 1999, a continuous daylight watch was maintained for an average of 3.6 days per week during the northern migration in June/mid August and the southern migration from late August/early November. The duration of the watch averaged 9.9h per day (standard deviation of 1.7h) for the 87 days of observation over the total period of 161 days (1 June to 9 November 1999). This average was 9.4h during the northern (43 days from June to mid August) and 10.4h during the southern migration (44 days from mid August to early November), reflecting the variation of daylight hours from 10.5h at the peak of the northern migration to 12.5h during the southern migration. The results for all years were normalised to the equivalent of a 10h period each day. Watches were abandoned only in extreme weather conditions such as continuous heavy rain or when onshore winds exceeded 40 knots. Optimal conditions prevailed in the cooler months when haze free days with light offshore winds were frequent. In the warmer months conditions were generally less favourable as haze

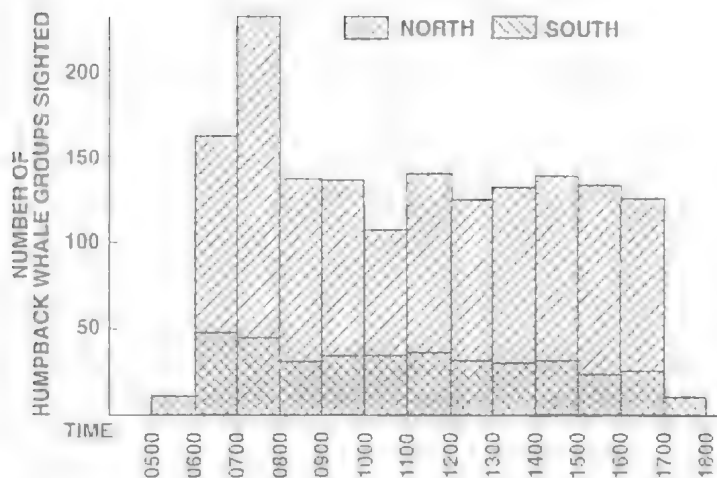


FIG. 1. Time of first sighting on an hourly basis of humpback whale groups observed from Point Lookout (1994-99).

associated with coastal pre-summer vegetation 'burnoffs' and northerly winds often detracted from atmospheric clarity. From an easterly location, such as Point Lookout, conditions were most favourable in the early morning when a whale blow was 'between' the low angle of the sun and the elevated shore position. Viewing conditions were less optimal, particularly on sunny days with choppy seas, between 0800 and 1130 when glare obliterated a large sector. Light rain and/or mist also were problems owing to the lack of contrast of a distant blow. Unseasonal winter rain in 1999 disrupted observations. A total of 250mm fell at Point Lookout during the last week of June and the first two weeks of July, the time of the expected northern migration peak. There were only six rain free days in that 21 day period.

A total of 3,653 (2,802 northbound and 851 southbound) humpback whales was seen during 1994-99, reflecting greater sighting effort during the northern migration in most years. The time of first sighting on an hourly basis, of the 1,588 northbound and 392 southbound groups which comprised that total is shown in Fig. 1. (A group of five was seen at 0444 on 9 November 1999, the last day of the study.) The higher sighting rate in the early morning is similar to that shown in and discussed by Paterson et al. (1994). They concluded that the high rate resulted from some whales remaining within visible range although they had reached Point Lookout before dawn, rather than a differential speed compared with the remaining daylight (or pre-dawn) hours. The potential effect of this factor on population

estimates will be discussed later. However, as it has been a constant finding since 1978 it would appear to have no effect on assessments of the rate of population increase.

Pairs and singles were the commonest group sizes in each migration phase (Fig. 2) with pairs dominating and not appreciably different (50.6% north and 52.6% south) in either phase. There were fewer singles (25.7%) in the southern compared with the northern (38.7%) phase. These findings were similar to those from 1978-92 (Paterson et al., 1994). Large groups were more frequent in the southern

migration but those >5 were uncommon in both phases (5.5% south and 1.0% north). The average group size was 1.76 north and 2.17 south.

The timing of the migrations past Point Lookout is shown on a weekly basis in Fig. 3 in conformity with Chittleborough (1965), Paterson & Paterson (1984, 1989) and Paterson et al. (1994). Most northbound humpback whales passed Point Lookout between mid June and mid July. The 'sharpest' peak in this study occurred in the first two weeks of July 1998. In 1999 observations were conducted from the first week of June until the second week of November. The southern migration was characterised by a less distinct peak similar to the findings in 1961 (Chittleborough, 1965) and 1987/92 (Paterson et al., 1994). The high proportion of mothers and

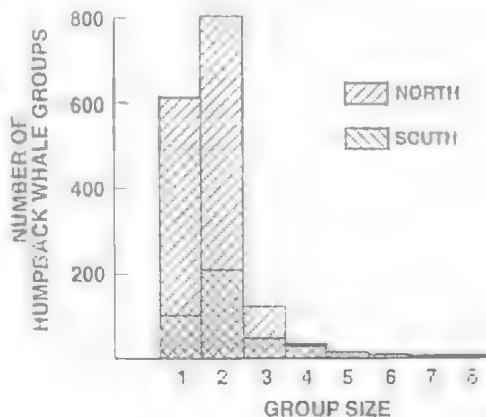


FIG. 2. Sizes of humpback whale groups observed from Point Lookout (1994-99).

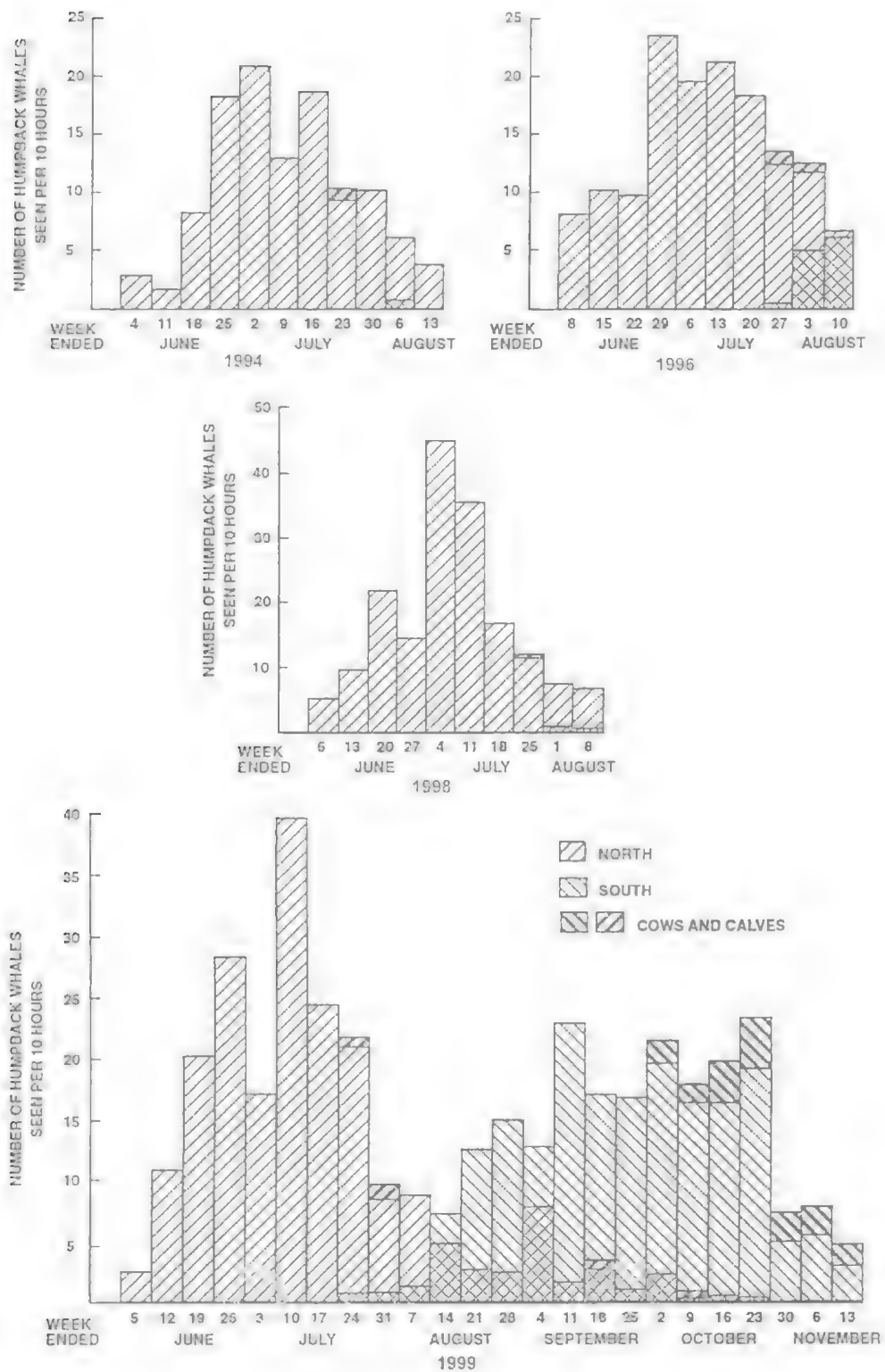


FIG. 3. Humpback whale sightings on a weekly basis observed from Point Lookout (1994-99).



TABLE 1. Proportion of stock passing Point Lookout in the periods shown at the peak of the northern migration.

Year	Proportion of stock passing at peak		
	4 weeks	8 weeks	10 weeks
1987	0.52	0.82	0.85
1992	0.50	0.80	0.86
1999	0.51	0.81	0.87

calves in the end-stage of the southern migration in those years is consistent with the studies of Dawbin (1966, 1997). Small numbers of northbound mothers and calves indicate that occasional calving occurs on the east Australian coast at latitudes higher than 18°-21°S where most calving is believed to occur (Simmons & Marsh, 1986; Paterson, 1991). In 1999 humpback whales migrating north past Point Lookout after the last week of August comprised 9% of the northbound total compared with 12% and 15% in 1987 and 1992 respectively (Paterson et al., 1994).

## STOCK STATUS

**RATE OF INCREASE.** The difficulties and limitations of estimating the rate of increase of this stock have been discussed by Paterson et al (1994) and Paterson & Paterson (1989). The survey techniques for the data reported here were constant throughout the period of observations. We use a similar procedure to that of Paterson et al (1994) in which the index chosen was the number of humpback whales observed per 10h averaged over the four weeks at the peak of the northern migration. Where there is a double peak (Fig. 3) the average was taken over the four consecutive weeks with the highest numbers. Data are available for all years from 1984 to 1999, except 1993, 1995 and 1997. In some years it was possible to estimate the average number of humpback whales passing over the eight and ten weeks at the peak of the northern migration, so these were also used as indices. Since the timing of the peak of the migration varied slightly each year, the actual dates of the weeks chosen varied from year to year. The periods of observation of the northern migration were as follows: 4 weeks in 1984, 5 weeks in 1985, 6 weeks in 1986, 8 weeks in 1988-90, 9 weeks in 1991, 11 weeks in 1994, and 10 weeks in 1996 and 1998. In 1987, 1992, and 1999 the observation period was at least 22 weeks, covering both the northern and southern migrations.

TABLE 2. Estimates of annual rate of increase and confidence intervals from data obtained over four, eight and ten weeks at the peak of the northern migration.

	Period at peak of northern migration		
	4 weeks	8 weeks	10 weeks
n	13	9	6
Years	1984-1992, 1994, 1996, 1998, 1999	1987-1989, 1991, 1992, 1994, 1996, 1998, 1999	1987, 1992, 1994, 1996, 1998, 1999
Rate of increase p.a.	11.1%	10.9%	10.7%
95% confidence interval	10.3 - 12.0%	10.2 - 11.6%	9.9 - 11.5%
99% confidence interval	9.9 - 12.4%	9.9 - 11.9%	9.3 - 12.1%
Correlation coefficient	0.994	0.998	0.999

To comply with the criteria of Bannister et al. (1991), it is necessary to assume that the proportion of the stock passing in the period chosen at the peak of the northern migration is constant from year to year. This assumption can be tested using the data of 1987, 1992 and 1994, when the observation period covered almost the full migration. The results in Table 1 show that the assumption is reasonable.

Figure 4 is a plot of the number of humpback whales per 10h averaged over the four, eight and ten weeks at the peak during the northern migration from 1984 to 1999. A logarithmic scale is used for the vertical axis so that a constant percentage increase appears as a straight line. The linear regression lines calculated using the logarithm of the number of humpback whales per 10h is also shown. These lines give the average annual rates of increase shown in Table 2. The three values are very similar compared with the range of the 95% or 99% confidence intervals.

Two factors that can be expected to affect the accuracy of the estimate are the number of weeks of data averaged in each year and the number of data points (years of observation) used in the calculation. More weeks of data should improve the estimate since a greater proportion of the stock would be included in the calculation. More data points would also increase the accuracy, since errors in sampling (e.g. due to fluctuations in the numbers of humpback whales passing from day to day and to variations in sighting conditions) would average out more with more data points. In the data presented, there is a trade off between these two effects, with the consequence that the average over the eight weeks at

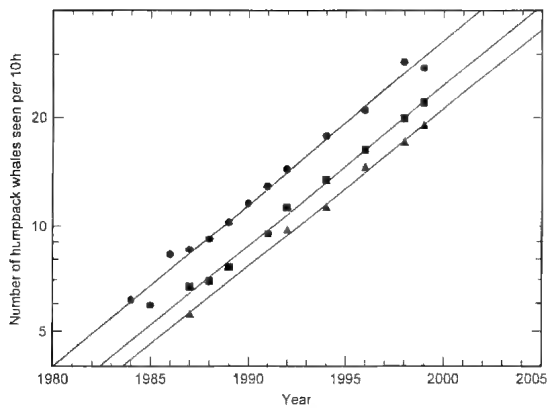


FIG. 4. Humpback whale sightings per 10h from Point Lookout averaged over the four weeks (circles), eight weeks (squares) and ten weeks (triangles) at the peak of the northern migration from 1984 to 1999. The regression line for each data set is shown.

the peak with nine data points provides the most accurate result. Since this result lies between the other two results, we chose it as the best estimate of the rate of increase: 10.9% with a 99% confidence interval of  $\pm 1\%$  about the mean.

**ESTIMATE OF STOCK SIZE FOR 1999.** The stock size for 1999 was estimated for the data from the northern migration using the same method that was applied to the 1992 observations and described by Paterson et al. (1994). It is assumed that the passage of humpback whales past Point Lookout is unaffected by whether it is day or night to the extent that, if it were possible to count whales passing at night, there would be no statistically significant difference between a series of observations at night and a series by day. Sampling was well distributed over the full period of 24 weeks, the number of sample units per week varying from 2 to 5 with a mean of 3.6. On this basis, and the reasons discussed by Paterson et al. (1994), the sampling is considered to be a reasonable approximation to random sampling of the stream of humpback whales passing Point Lookout. The day-by-day fluctuations in numbers passing are shown in Fig. 5.

Because of the long term rise and fall in numbers over the course of the migration (Figs 3, 5), there are advantages in using stratified random sampling theory (Cochran, 1963). The sample was split into 11 equal strata, each comprising two weeks of observations, the first stratum being the fortnight ending on 12 June and the 11th being the fortnight ending on 30 October (the last fortnight in which northbound humpback

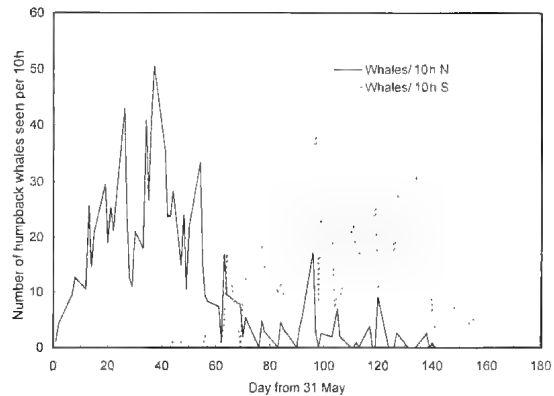


FIG. 5. Humpback whale sightings during each observation day at Point Lookout (1999).

whales were seen). The number of humpback whales seen per 10h in an equivalent 10h observation period is considered to be a sample unit. Over the 154 days of the 11 strata, there were approximately 370 10h periods (total number of hours in 154 days, divided by 10). The sample can then be considered to be the selection of those 10h periods when observations were actually made. This gives a total of 81 sample units.

From Cochran's equation 5.14, the estimate of the total population from which the sample was drawn, with 95% confidence interval, is

$$N \bar{y}_{st} \pm t N s(\bar{y}_{st})$$

Here  $N = 369.6$  is the number of equivalent 10h units in the total period of 154 days over which the observations were made and

$$\bar{y}_{st} = \sum_{h=1}^3 N_h \bar{y}_h / N \quad \text{is the weighted mean}$$

(Cochran's equation 5.1), where  $\bar{y}_h$  is the sample mean and  $N_h$  the total number of units in stratum  $h$ .

Also, from Cochran's equation 5.11,

$$s^2(\bar{y}_{st}) = \sum_{h=1}^3 N_h (N_h - n_h) s_h^2 / (N^2 n_h)$$

is the estimate of the variance of  $\bar{y}_{st}$ , where  $s_h^2$  is the sample variance in stratum  $h$ . The value of  $t$  is Student's  $t$  for the effective number of degrees of freedom given by Cochran's equation 5.15.

The resulting estimate of the stock size with 95% confidence interval is  $3,599 \pm 437$ , which we round off to  $3,600 \pm 440$ .

This may be compared with the estimate from

Point Lookout observations of the 1992 northern migration of  $1,896 \pm 253$ , determined using the same technique (Paterson et al., 1994). This increase in stock size over seven years is equivalent to an average yearly rate of increase of 9.6%, slightly lower than the estimates of the previous section which were based on data over a number of years. The data points for 1992 (Fig. 4) are slightly higher than the regression line, while those of 1999 are slightly lower, so the average rate of increase determined using only the 1992 and 1999 data points would be lower than those of the regression lines. The average rate determined from these two data points for the ten weeks at the peak of the migration, is 10.1%. The unfavourable weather conditions during 1999 are probably part of the reason that the data points for this year are below their regression lines, and is most pronounced in the point for the peak four weeks, which had unusually prolonged periods of rain. A number of factors may cause fluctuations in the data points about the regression lines of Fig. 4, including variation in sighting conditions. The value of the regression analysis is that it minimises the effect of these fluctuations, and the more data points used in the calculation, the better the accuracy. Thus the regression lines of Fig. 4 are considered to give a better estimate of the rate of increase than the comparison of the stock sizes for 1992 and 1999.

#### DISCUSSION

The International Whaling Commission (IWC) banned the capture of humpback whales in the Southern Hemisphere in 1963 but, at that time, was unaware of the extent of illegal Russian Antarctic whaling, particularly in Area V. It was not until more than 30 years later that reports of captures in the order of 15,000 in excess of IWC quotas in Area V between 1959-62 were published (Yablokov, 1994; Tormosov, 1995; Mikhalev, 2000).

Chittleborough (1965) and Chapman (1974) estimated the surviving Area V stock at 500 and 200 respectively, based on captures known at the time. Paterson et al. (1994) suggested that fewer than 100 may have survived on the east Australian coast, based on extrapolation back to 1962 (the cessation of east coast whaling) of the trend in numbers observed off Point Lookout from 1984 to 1992. The precise numbers of the survivors will never be known but it is clear that the population was catastrophically low. It is a tribute to the resilience of this species that it has been able to recover at the rates discussed above.

In that respect it should be noted that Chaloupka & Osmond (1999) estimated that the number of humpback whales observed in the Great Barrier Reef region increased at an average annual rate of only 3.9% from 1982-95 (95% confidence interval 1.9-5.7%), based on reports of sightings of opportunity made during flights for coastwatch and marine park management. However, the rate of increase in the present study is similar to that of Bryden (1990) which was calculated from surveys conducted independently of ours at Point Lookout. This location, as well as other elevated shore-positions at similar latitudes on the east Australian coast, offers an excellent platform of opportunity to assess further recovery in this population of humpback whales.

Our estimates of stock size and rate of increase apply only to that component of the Area V stock that migrates past Point Lookout and may be considered representative of the stock that migrates along the Australian coast near its most easterly point. The consistent rate of increase, evident in the very small deviation of points from the regression line (Fig. 4), suggests that this component is relatively self contained with very little interchange with other stocks. This is consistent with the small percentage of interchange between stocks in the Australian and New Zealand region noted from recapture of *Discovery* marks during whaling (Dawbin, 1966).

Brown et al. (1995) inferred that a significant proportion of female humpback whales do not migrate, based on biopsy studies off Point Lookout which showed a higher proportion of males than females. They suggested that observed rates of increase may be confounded by a change in the proportion of a population that is migrating. Our results are an estimate of the rate of increase of the proportion migrating, and again the consistency of the results over a 16 year period (Fig. 4) suggests that, if some proportion of the stock does not migrate, it does not vary significantly from year to year, and therefore would not significantly affect the observed rate of increase. An alternative hypothesis, that part of the observed trend has resulted from a consistent change in the proportion of stock migrating, seems unlikely.

A shore-based method such as ours relies on certain assumptions that could affect the population estimate. We assumed that all humpback whales passing Point Lookout were within visual range, whereas Bryden (1985) found that ~5% passed at distances >10km which is

considered to be the limit of visual range (apart from breaching whales), and some may not have been seen at closer ranges due to poor visibility. Factors such as these have been discussed by Findlay & Best (1996a, 1996b) who conducted shore-based observations from Cape Vidal in South Africa from 1988 to 1991. They considered that shore-based observations give minimum total population estimates because some whales pass beyond observer visibility and there are variations in sighting probabilities within the range of observer visibility. The higher than average sighting rate early in the day (Fig. 1) has been previously discussed (Paterson et al., 1994), and was considered to overestimate the stock size by ~5.5%, based on data from 1978 to 1992. On the other hand, the effect of mid morning glare tends to reduce the sighting rate between 1000–1100 (Fig. 1). For the data period 1994 to 1999 (Fig. 1), the effect of these two variations in sighting rate is considered to overestimate the stock size by ~5.7%. Another factor is that the estimate ignores the numbers of humpback whales passing outside the period of observation. In 1999, it is evident from Fig. 5 that the number passing after the observation period would be negligible, and, based on the factors discussed by Paterson et al. (1994), those passing before the observation period would be small, probably ~2%.

The post-whaling recovery of the east Australian humpback whale stock continues at a rate in the order of 10% and shows no signs of slowing. There is anecdotal evidence that numbers for the New Zealand portion of the Area V stock are still very low. There is, however, acoustic evidence that humpback whales still pass near New Zealand since a song was recorded off Kaikoura in July 1994 (Helweg et al., 1998). A dedicated survey, possibly from the elevated shore position at the former Cook Strait whaling station, may help to resolve the issue concerning the present status of the New Zealand stock.

The ultimate size of the east Australian stock will of course depend on extrinsic and intrinsic factors. The resilience of this species is evident from the above data but as yet imponderable external factors such as climate change, over harvesting of krill (the food source of Southern Hemisphere humpback whales) and the possible resumption of whaling are matters of future concern for the long term well being of this stock as well as the other stocks of Southern Hemisphere humpback whales which were devastated in the modern whaling era.

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## SOUTHERN HEMISPHERE GROUP IV HUMPBACK WHALES: THEIR STATUS FROM RECENT AERIAL SURVEY

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From 1976 to 1994, aerial surveys of Southern Hemisphere 'Group IV' humpback whales, *Megaptera novaeangliae*, were undertaken to provide relative abundance indices of animals migrating northward along the Western Australian coast. These demonstrated a high rate of population increase, at least between 1982 and 1991, of ~10% per year. Surveys were conducted over 10 'good' days in mid-July in an area off Shark Bay, WA, where humpback whales were taken in the last years of Australian whaling, to 1963. The 1994 survey confirmed the increase rate with an estimated population of 4-5,000. The most recent survey, in 1999, planned to obtain an estimate of absolute abundance, was considerably affected by poor weather (only 15 'good' days' flying were possible out of 30 planned over two months). Nevertheless, applying a correction factor for animals missed while submerged to the estimated number of animals sighted gives the 1999 population size within 8,207-13,640. The result is dependent on 'deep diving' time and would be proportionally lower should this dive time be less than the range used (10-15 minutes). We review reported rates of increase and population estimates for this stock in the Antarctic, as well as preliminary Southern Hemisphere population estimates that take account of much larger than officially reported catches in the 1950s-60s. Plans for future surveys are discussed. The population's exploitation history is briefly reviewed. □ *Humpback whale, aerial survey, population estimate, recovery, Western Australia.*

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Since 1976 aerial surveys have been conducted off Shark Bay, Western Australia, to investigate possible increase in numbers in the Southern Hemisphere humpback whale, *Megaptera novaeangliae*, Group IV population. That population, summering in the Antarctic between ~80°E-120°E, and wintering off the coast of WA, was severely depleted by whaling twice in the 20th Century, in 1934-1939 and 1949-1963. When Australian humpback whaling ceased in 1963, the population was calculated to have been reduced to 3.5-5% of its pre-1935 state.

Following increasing reports of humpback whale sightings off the WA coast in the early-mid-1970s, surveys of animals during their northward migration were undertaken from Carnarvon (24°52'S, 113°38'E) in an area off Shark Bay. These findings served for comparison with aerial spotter and other data from operations there in the last year of whaling.

This paper reviews the results of aerial surveys from 1976-1999 in the context of estimates of initial population size, recent results from Antarctic surveys and preliminary estimates of current Southern Hemisphere stock sizes.

### HISTORY OF EXPLOITATION

Humpback whales were the first Southern Hemisphere whale species to be taken during 'modern' whaling, using steam catcher boats and explosive harpoons. Starting in 1904 at South Georgia, large catches were obtained in the early years, followed by a rapid decline (Mackintosh, 1965). By 1916 some 38,000 animals had been taken in the western South Atlantic (Findlay et al., 2000), with ~8,000 in 1910 and 1911. Over 16,000 were also taken from 1909-1914 on the west coast of South Africa.

'Modern' whaling of humpback whales off Australia began in 1912 (Dakin, 1963). Before that, as elsewhere, 19th Century 'open boat' whalers (using hand harpoons and based on pelagic sailing vessels or from shore), had taken humpback whales but not generally as the preferred prey. Although coastal in habit, at least during their winter migrations, humpback whales were harder to catch than slower moving right whales (*Eubalaena australis*). Their oil was not as sought after as that from right or sperm (*Physeter macrocephalus*) whales, and their relatively short and inflexible baleen was not as

valuable as that of right whales. Nevertheless, catches were taken by pelagic whalers on the breeding grounds, for example off Dampier Archipelago, NW Australia, and some during their migration along WA coasts (Bannister, 1986).

'Australian' humpback whales have been generally regarded as belonging to two populations, separated during the breeding season by the Australian continent, and, despite a small amount of mixing, feeding on generally separated Antarctic feeding grounds. Animals breeding off the WA coast belong to the Southern Hemisphere 'Group IV' population, while those off the east coast belong to 'Group V'. These appellations were first used by Mackintosh (1942), the word 'Group' denoting a population occupying a tropical breeding ground and a feeding area (in the Antarctic) to the south. These were based on whale marking results: in the case of Group IV animals, individuals marked while feeding in summer in the Antarctic between 80°-100°E were caught in winter off the WA coast, at ~113°E (Rayner, 1940). The assumption has been that in common with other Southern Hemisphere humpback whales, the Group IV breeding ground is concentrated close to the coast (in this case of WA). In temperate and tropical waters, catches and sightings in both the 19th and 20th Centuries were coastal, suggesting that the animals concentrated near shore and were not evenly distributed across open oceans (Dawbin, 1966). Mackintosh originally recognised five groups, with animals migrating between Antarctic feeding grounds and warmer-water breeding grounds off Chile, in the South Atlantic, off South Africa, off western Australia and off eastern Australia/New Zealand. Their formal longitudinal limits were taken from known baleen whale feeding grounds, including those of humpback whales. The Group IV population was thus designated as occurring between 70°E-130°E. In 1965, Mackintosh amended his five groups to six, to include two in the South Atlantic, one wintering off Brazil, the other off western Africa. More recently, seven major groups have been suggested (International Whaling Commission, 1998a), including one in the central South Pacific, but the distinction between animals wintering off the west and east coasts of Australia remains.

Twentieth Century humpback whaling on the Group IV population off the WA coast occurred in three main phases: i) 1912-1916, 1922-1928, with shore-based catches mainly from Norwegian Bay/Point Cloates, NW Australia (Dakin, 1963;

Chittleborough, 1965); ii) 1935-1939, pelagic catches off the W coast (Chittleborough, 1965); and iii) 1949-1963, shore-based catches from Point Cloates (1949-1955) and Carnarvon (1950-1963) on the W coast, and from Albany (1952-1963) on the S coast (Chittleborough, 1965; Bannister, 1964).

The major catches were taken in the pre- and post-WWII periods 1935-1939 and 1949-1963. Chittleborough (1965) records 7,244 animals taken off WA in the former and 12,312 to 1962 in the latter. A further 87 were caught in 1963 (Bannister, 1964).

In addition, between 1928-1938 and from 1948 to at least 1963, there was pelagic whaling on the Group IV population at the other end of the migration, on the Antarctic feeding grounds. Prior to WWII ~6,000 animals were taken, and post-WWII a similar number was officially recorded as caught between 1950-1962 (Chittleborough, 1965). By 1963, the stock decline resulting from catching at both ends of the migration was so severe that whaling had become uneconomical and Australian humpback whaling ceased.

Chittleborough (1965) calculated that the Group IV stock depletion to 1962 could have been from a high of 17,000 animals prior to 1935, from ~10,000 in 1949, and to fewer than 800 animals at the end of 1962. Including the 1963 catch, the decline was calculated as to ~600 by the end of that year (Bannister 1964).

Revelations of unreported illegal Southern Hemisphere pelagic catches by Soviet fleets before and after 1963 (Yablokov, 1994) have led to a considerable revision of the catch figures. The overall Group IV catch is now estimated as ~17,040 for 1947-1963, and ~480 for 1964-1967 (Findlay et al., 2000, tables I and II, where 'breeding stock D' is equivalent to Group IV, except that for catches south of 40°S, those for Group IV have been taken as occurring between 60°E-120°E, [IWC, 1998a]). The revision of the Group V population (~ 'breeding stock E' in Findlay et al., 2000, but between 120°E-170°W, south of 40°S) is even higher. Chittleborough (1965) believed that to explain the very high mortality coefficients he obtained for that population over the short period 1959-1962 there must have been unreported catches in the order of 5,000 in 1961 and 1962. In fact, for the Group V population the true total catch for 1959-1962 is estimated as 15,975 (Findlay et al., 2000), compared with 3,918 reported at the time (Chittleborough, 1965); for the years 1961-1962



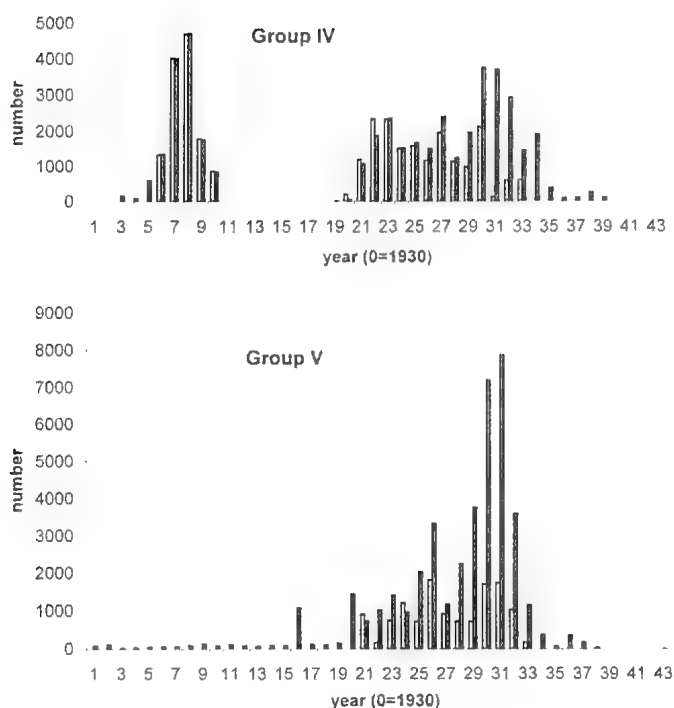


FIG. 1. Comparison of 'official' (light column) and actual (dark column) catches from the Group IV and Group V populations, 1930-72.

it is 3,549 compared with 1,483. For that stock, and for Group IV, considerable illegal catching had been occurring even earlier than Chittleborough supposed. It should be noted however that at least two Group V substocks have been recognised, from their breeding ground distribution, one centred on the Australian east coast, the other on Fiji/Tonga (Dawbin, 1966). Chittleborough's Group V population estimate was based largely on a breeding component on the east Australian coast and a feeding component between 130°E-170°W. A comparison of reported and actual catches for both stocks is given in Fig. 1.

#### AERIAL SURVEYS

**1976-1994 SURVEYS.** An indication of the very low humpback whale stock levels in the mid-1960's was given by the results of a survey for sperm whales off the WA coast, flown at monthly intervals from April 1963 to March 1965 (Bannister, 1968). Only ten humpback whale contacts were recorded. The flight path covered an area seawards of the continental shelf, but observations were made from the shoreline off Shark Bay, Geraldton, Perth and Albany, thus

covering the humpback whales' north and south migration routes. From then until the early 1970s there were few, if any, reports of sightings along the WA coast, in line with the conclusion of Findlay et al. (2000) that Southern Hemisphere stocks were at their lowest level in about 1968 — perhaps less than 1,000 animals.

In winters of the mid-1970's reports began of humpback whale sightings off WA in former concentration areas such as Shark Bay. Aerial surveys were conducted there annually from 1976-1978 and repeated in 1980, 1982 and approximately every three years thereafter (Bannister, 1985). Surveys were designed to cover the area searched by the whaling operations, particularly outside Shark Bay, where catching had been concentrated in 1963, the last year of whaling there. From 1982 each survey covered the same area, with the same flight path, type of aircraft and, as far as possible, the same pilot and observer. Each took place over ten 'good' flying days in mid-July when the maximum number of animals would be moving northward through the area.

Results to 1988 (Bannister et al., 1991) showed significantly more humpback whale sightings in the area in the 1980's than in 1963. Further surveys, in 1991 and 1994, demonstrated annual increase rates of ~10% (instantaneous rates, obtained from the regression of  $\log n$  of the average number seen per flying day each year, of  $10.09 \pm 3.0\%$ ,  $10.00 \pm 4.6\%$  respectively; Bannister, 1994, 1995). Using a log-transformation of the number seen on each flying day in each year, 1982-1994, the annual rate was  $10.15 \pm 4.6\%$  (Fig. 2). Such high population growth rates, i.e.  $\geq 10\%$ , are considered to be within the maximum biologically possible (IWC, 1998b) and are feasible if: the average pregnancy rate is 0.5; survival rates are high (at least 0.96); and the age at first parturition is relatively low, i.e. at a maximum of 8 years (Brandao et al., 2000).

By comparison with the estimated population of 568 at the end of 1963 (Bannister, 1964), the size in 1994 was estimated at 4-5,000 (Bannister, 1995).

The 1994 survey results indicated that to detect

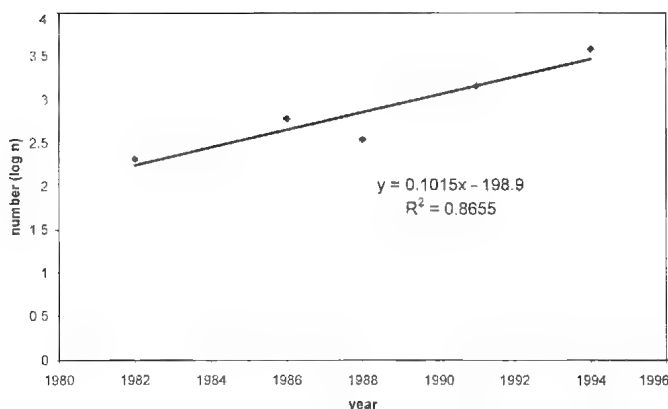


FIG. 2. Aerial survey, outside Shark Bay, 1982-94: regression of sighting rates per flying day (log-transformed, i.e.  $\text{Log } n$ ) per year.

a significant difference in population size in future years, at an annual rate of 10%, an interval of three years would be required between surveys (N. Caputi, in Bannister, 1995). Given funding constraints, that survey was carried out in 1999.

**1999 SURVEY.** Previous surveys, originating in 1976 and modified in 1982, were designed to provide a relative index of abundance over a relatively short period (ten 'good' flying days) in mid-July, during the animals' northward migration. That period was chosen on consideration of expected weather conditions and for comparison with available commercial whaling spotter data, and when most (70%) humpback whales would be moving northwards.

By contrast, the 1999 survey (Bannister & Burton, 2000) was designed to provide an absolute abundance estimate of northward-moving animals, in the same area, but over a longer (~2-month) period than earlier surveys. It used a Partenavia P68B high-wing, twin-engine aircraft (Tropicair Services Pty Ltd) flying at 120 knots and 1500 feet, with two observers, one on either side of the aircraft, seated behind the pilot. Bubble observation windows were fitted to maximise the area swept, particularly to cover the area immediately below the aircraft. A GPS and on-board computer system were available. To measure angles to sightings a clinometer (industry standard Suunto PM-5/360PC) was used for declination, and an angleboard for horizontal angles.

Difficulties with the availability and fitting of the bubble windows and associated airworthiness led to the first two flights taking place without them.

To allow for comparability with earlier results, the same transect grid was flown as in all surveys since 1982, i.e. approximately  $80 \times 30$  nautical miles immediately W of Bernier, Dorre and Dirk Hartog Islands on the western boundary of Shark Bay, between  $112^{\circ}30' - 113^{\circ}10'E$  and  $24^{\circ}46' - 26^{\circ}09'S$  (Fig. 3). The N-S distance between gridlines varied between 7-8nm.

To examine the extent of coverage of the humpback whale migration path, transects were extended seawards of the area on two occasions, out to the operational limits of the aircraft (to  $112^{\circ}14.1'E$ ), 50nm W of the northern tip of Bernier I., i.e. 20nm W of the normal seaward limit of the survey at that latitude.

To examine the distribution of humpback whales within Shark Bay, which earlier surveys suggested was a 'resting area' for migrating individuals, flights were conducted in an area  $\sim 70 \times 30\text{nm}$  between  $113^{\circ}04' - 113^{\circ}35'E$  and  $24^{\circ}58' - 25^{\circ}32'S$ , within the bay. All analyses in this paper, however, refer to animals in the area 'outside the bay', where they are assumed to be actively migrating.

Based on a review of migration patterns off western and eastern Australia (Chittleborough, 1965; Bryden et al., 1996; Dawbin 1997) the two month period between 15 June and 15 August was chosen for the survey, during which the majority of northward-migrating humpback whales could be expected to traverse the area. For logistical reasons (availability of observers and aircraft) the period was later amended to 21 June-20 August. Thirty flights (one every second day) were proposed, but it was decided to allow for possible comparison with earlier survey data (i.e. to 1994), by including a period of flights on ten consecutive days over 9-18 July (the 'comparable ten-day period'). On that basis, taking account of the probable changing density of whales over the two months, a variable sampling regime was planned. This required sampling every two days towards the beginning and end of the two months (when numbers could be expected to be relatively low) and — apart from the mid-July 'comparable ten-day period' — every three days towards the middle (when numbers should be higher), while still providing 30 flying days overall.

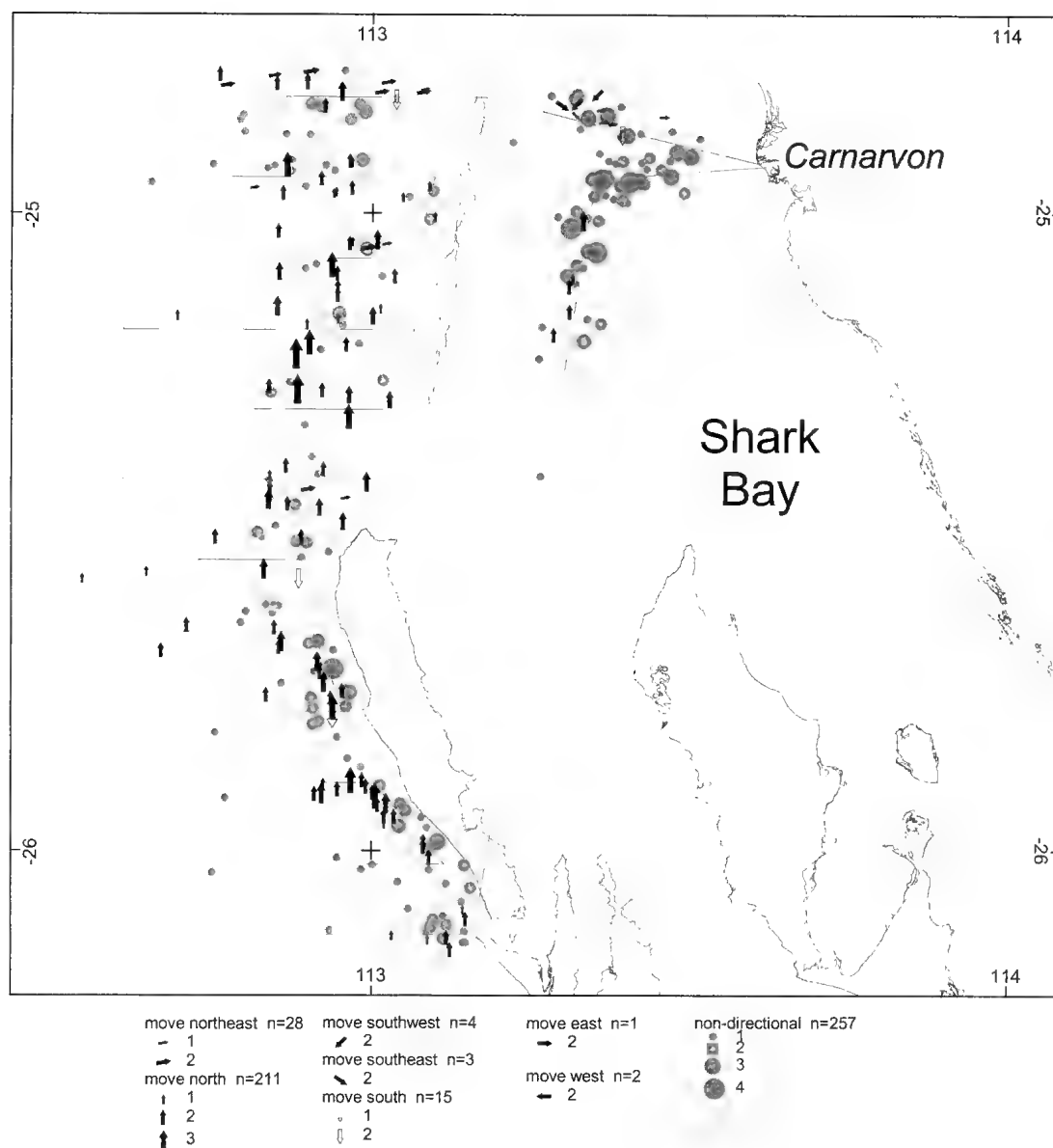


FIG. 3. Aerial Survey, outside Shark Bay, 1999: flight path, sighting positions, numbers and directions of humpback whale movement for the six completed flights within the 'comparable ten-day period', 9-18 July.

## RESULTS

**FIELDWORK.** The planned start date (21 June 1999) was delayed to 24 June, through observer availability and for fitting of bubble windows. The finishing date (20 August) was brought forward to 19 August, again because of observer availability.

Planned coverage of 30 flying days was not achieved because of poor weather conditions —

the proportion of 'good' flying days, particularly consecutive ones, was low. Survey days were restricted to those with wind speeds of <15 knots. Only 18 flights could be attempted in those conditions, and of those, 15 were completed, the remaining 3 being terminated early because of deteriorating weather. For the first of the 15 completed days the bubble windows were not available. For the 'comparable ten-day period',

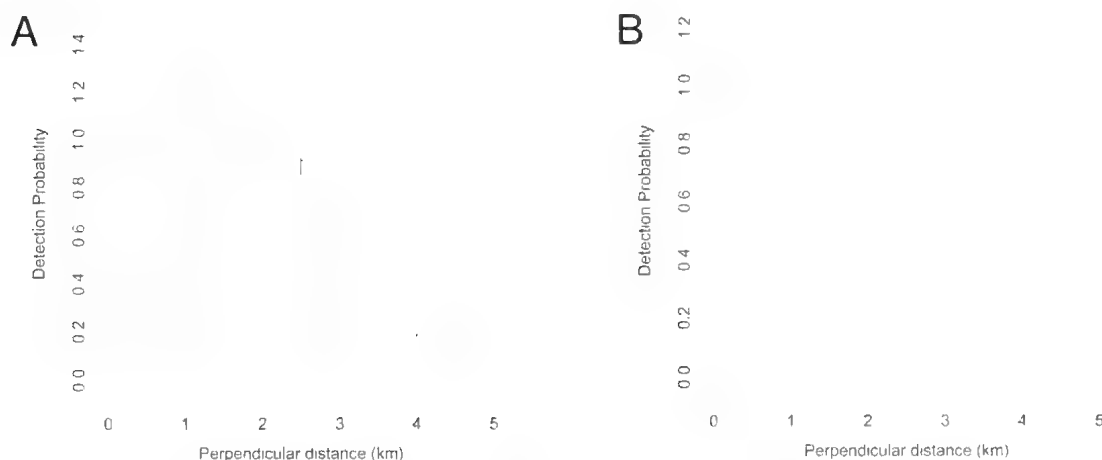


FIG. 4. Aerial survey, outside Shark Bay, 1999: estimation of strip-width. Fitted detection function for chosen (Hazard Rate) model: A, based on exact perpendicular distances; B, based on selected cut-points.

9-18 July, only six complete flights were possible due to bad weather. The extended legs seawards of the main search area were flown as planned, on two occasions, 4 and 27 July.

An example of the results obtained is given in Fig. 3, which shows the flight path and distribution of sightings for the combined 'outside the bay' data for the six completed flights within the 'comparable ten-day period', 9-18 July.

**DATA ANALYSIS. Population Size.** Data from the 14 'good' days flown (excluding the one without bubble windows) were analysed by combining standard aerial line transect methodology with a migration count approach (Bannister & Hedley, 2000). Effective strip width was estimated by pooling data from all flights using DISTANCE software (Laake et al., 1995), which also gave an estimate of mean pod size. The number of pods passing through the surveyed area was then estimated from the daily counts using a FORTRAN program, GWNORM (Buckland, 1992), which fits a density function based on a key function (usually a Normal distribution) and Hermite polynomial adjustment terms, by maximum likelihood methods. Outputs from the line transect analysis and the migration modelling were combined to obtain an estimate of the number of individual whales passing through the survey area during the migration period.

Estimated strip half-width was 3.34 km, from a hazard rate model chosen as the 'best' model from four fitted, using Akaike's Information Criterion (Akaike, 1973). Difficulty was experienced initially through significant lack-of-fit for small

distances (Fig. 4A) for the candidate model chosen. Clearly the observers, even with bubble windows fitted, either could not see directly beneath the aircraft, or found it preferable to scan out to the horizon and focus on areas further away from the trackline. As a result, for the analysis the data were grouped (Fig. 4B). Estimated mean pod size was 1.87 (95% CI 1.7894, 1.9588); because there was evidence that recorded pod size decreased with perpendicular distance from the transect line, the estimate was obtained from a regression of log (pod size) against perpendicular distance.

In fitting migration models to the daily pod counts, it was assumed that the rate of passage of the whales through the survey area was such that no whale seen on one day would be available for detection on the subsequent day. With the northern and southern boundaries ~90 nm apart, an animal would have to travel at an average speed of less than 3.78 knots for the assumption not to hold. Four alternative scenarios were considered (Fig. 5A-D) to allow for analyses of two sets of data (from E-W legs only; from all transects, i.e. including N-S legs) in two different migration periods (80 days, 11 June-1 Sept.; 100 days, 1 June-8 Sept.). The migration periods were based on Group V Australian coastal surveys where there has been some variation in length of the observed northward migration (75-85 days, Paterson et al., 2001; up to 110 days, Bryden et al., 1996). While adding the N-S transects increases the data available for analysis, the use of E-W legs only is preferred, because the analysis relies on the random placement of transects with respect to the whales' distribution.

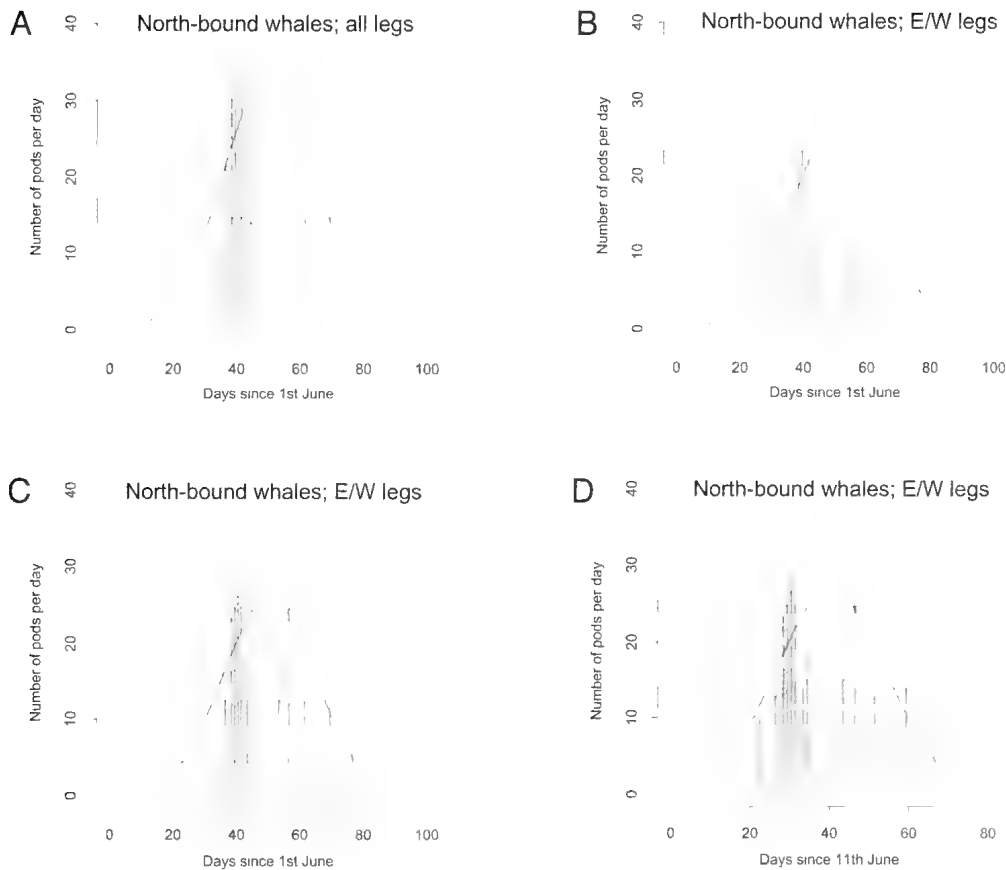


FIG. 5. Aerial survey, outside Shark Bay, 1999: A-D, pods sighted on 'completed' days, together with fitted curves, for combinations of transects (legs) and migration periods.

The E-W transects, being perpendicular to the marked density gradient (with higher densities near the coast and being latitudinally systematically spaced throughout the area [Fig. 3]), provide representative coverage; that is not the case for the N-S transects, use of which gives a biased estimation. Results for the four scenarios (Table 1) give point estimates ranging from 3,249 to 3,441 with 95% CI, with a lower bound of 2,706 and upper bound of 4,294.

Two major factors influenced the 1999 estimate, one operational, the other analytical:

i) Data quality. Given the 60 days allocated for the survey and the planned coverage of 30 flights, the number of completed flights (14) is small for fitting to a migration model, particularly given the unevenness of the coverage. Also, the expected peak of the migration (around mid-July) was inadequately sampled. In addition, the weather early in the period of completed flights, judged

by wind speed, was generally worse than later. Modal wind speed for the first three completed flights (3, 4, 7 July) was ~12 knots (range 10-16 knots) compared with 8 knots (range 0-12 knots) thereafter; thus it is likely that there was some undercounting in the earlier part.

ii) Estimate of  $g(0)$ . The probability of detecting animals on the trackline,  $g(0)$ , was not taken into account in earlier surveys where relative abundance indices were the objective. For the

TABLE 1. Aerial survey estimates of population size, 'outside' Shark Bay, Western Australia, 1999, northbound animals only. \*Number of animals; \*\* 95% C.I.

Legs	80 day period (11 June-1 Sept)		100 day period (1 June-8 Sept)	
	Estimate*	Range**	Estimate*	Range**
E-W	3,365	2,706-4,185	3,441	2,757-4,294
All	3,249	2,720-3,881	3,434	2,864-4,117

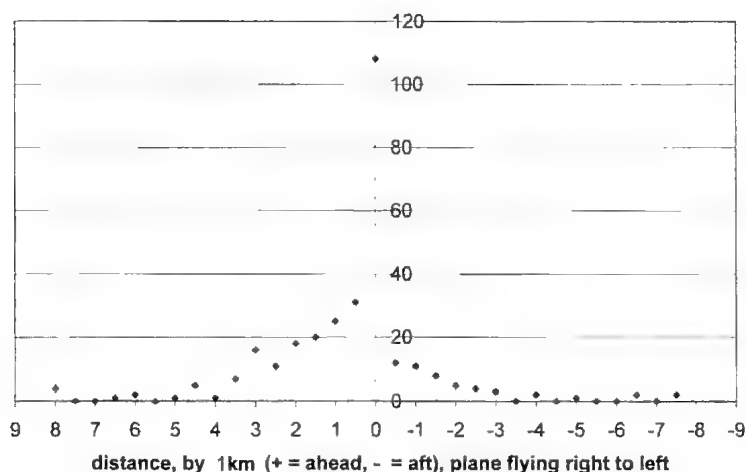


FIG. 6. Aerial survey, outside Shark Bay, 1999: distribution of sighting distances ahead, abeam and aft of the observers, over the six 'good' days, 9-18 July.

1999 survey, where the intention was to obtain an absolute estimate, and given that whales generally spend a considerably longer time under water than at the surface, a knowledge of  $g(0)$  is essential. Barlow et al. (1988) derived a correction factor for the probability of missing submerged animals during aerial surveys of eastern Pacific harbour porpoises as:

$$\text{Pr}(\text{being visible}) = (s+t)/(s+d)$$

where  $s$  = average time an animal stays at the surface,  $d$  = average time spent below the surface (i.e. 'deep-diving'), and  $t$  = window of time during which an animal is within the visual range of an observer.

Applying the above for humpback whales, values for  $s$ ,  $t$  and  $d$  can be estimated with varying degrees of precision. Migrating humpback whales off the WA coast are reported to blow several times at the surface over a period of ~2-5 minutes and then dive for ~10-15 minutes (C. Jenner, C. Burton, pers. comm.). Those observations correspond with the 'longer, presumably deeper, dives of 8 to 15 minutes ... [surfacing] between dives for about 4 minutes, blowing regularly' reported for humpback whales by Winn & Reichley (1985). Information from the Australian east coast, however, suggests that diving intervals may be shorter, with deeper dives ranging from as little as 2 or 3 minutes to 5 or 10 minutes (M. Bryden, R. Paterson, pers. comm.), with larger groups of animals, i.e. 3 or more, diving more frequently than single animals or pairs (M. Brown, pers. comm.). We have taken  $s$  for west coast animals as ~2-5mins and  $d$  as

~10-15mins, bearing in mind that  $d$ , at least, may be overestimated.

To obtain  $t$ , a subset of observations of declination and horizontal angles, comprising those obtained during the west coast 1999 survey 'comparable ten-day period', 9-18 July, has been used to provide information on the distance from the aircraft at which sightings were made. In this case the distance calculated was parallel to the cruise track, and not perpendicular to it as in the calculation of strip-width above. The results (Fig. 6) show that a high proportion of sightings was made directly abeam; that may be less a function of the distance

at which the animals occurred than the time taken to make the measurements. From the results as presented, a maximum value for the sighting 'window' can be estimated at ~8km, comprising animals seen ahead (generally up to 5km), abeam and aft (up to 3km).

However, estimation of  $g(0)$  by this method requires the assumption of a rectangular 'availability window' in which a whale pod at a given perpendicular distance is equally likely to surface at any distance along the length of the window, i.e. parallel to the transect line. Although sightings were clearly peaked abeam (thus violating the assumption), that seems likely to have been caused by the way the measurements were obtained, as noted above. Smoothing the data by eye to obtain a more appropriate idea of the likely rectangular sighting window suggests its length might be less than 8km, i.e. forward to 3.5km and back only to 1km, giving a 'window' of 4.5km, which can be taken as a minimum estimate. At 120 knots, 8km would be covered in 2.2 minutes, and 4.5km in 1.2 minutes.

Minimum and maximum values for the three variables are then:  $s = 2, 5$ ;  $d = 10, 15$  (although the true minimum value may be <10);  $t = 1.2, 2.2$ .

The longer the time the whale spends at the surface ( $s$ ), and the shorter the time spent deep-diving ( $d$ ), the greater the probability of seeing all animals present; the converse is true for the sighting 'window' ( $t$ ). The most conservative population estimate is that derived by using the highest probability of detecting animals, while

the least conservative is that derived using the corresponding lowest probability. However, these probabilities are unknown, and the data are insufficient to estimate them accurately. Given the uncertainties, the likely 'highest' probability ( $Pr_{max}$ ) has been estimated using  $s = 5$ ,  $d = 10$ ,  $t = 1.2$ , and the likely 'lowest' probability ( $Pr_{min}$ ) with  $s = 2$ ,  $d = 15$ ,  $t = 2.2$ , noting that other values for these parameters are also potentially feasible (e.g.  $d < 10$ ) and may thus extend the range of detection probabilities.

Then  $Pr_{max} = (5 + 1.2)/(5 + 10)$  i.e. 0.41; while  $Pr_{min} = (2 + 2.2)/(2 + 15)$  i.e. 0.25.

Applying those factors to the more conservative of estimates in Table 1 (that for the 80 day period and E-W legs only, 3,365) gives a minimum adjusted population estimate of 8,207 and a maximum of 13,460. If  $d$  were indeed  $< 10$ , the minimum estimate could be lower, but it is not possible to say by how much. If, for example,  $d$  were as low as 5, the probability of detecting the animals on the trackline would be increased to 0.62, and the adjusted population size would be reduced to 5,427.

It seems appropriate to conclude that the population passing through the survey area in 1999 would have numbered more than the most conservative estimate unadjusted for  $g(0)$ , i.e. 3,365. With 'deep diving time',  $d$ , of 10-15 minutes, the 1999 population size lies within the range 8,207-13,460. However, should  $d$  indeed be closer to 5 minutes than 10, the lower bound could be 5,427.

From the most recent survey results (Paterson et al., 2001) of animals migrating along the Australian east coast past Stradbroke Island, Queensland, Group V population size (at least as it refers to animals migrating along the Australian east coast) in 1999 was  $3,600 \pm 440$  (95% CI). Another east coast survey, in 1999, did not yield conclusive results (M. Brown, pers. comm.): poor weather led to a lack of observations at the migration peak. But based on a successful survey in 1996, and at an increase rate of 12.3% (Bryden et al., 1996), that part of the Group V population size in 2000 would be  $\sim 4,600$ . The Group IV (Antarctic Area IV and Australian west coast) population has generally been considered larger than that of the Group V (Antarctic Area V and Australian east coast) population, by some 20-70% (Chittleborough, 1965). On that basis the two recent Group V results would imply a 1999 Group IV population size of 4,300-7,800, i.e. somewhat less than the

range calculated with a diving time of 10-15 minutes.

In all the above it has been assumed that an estimate of the number of animals passing 'outside' Shark Bay for the full extent of the northward migration will be a true estimate of Group IV population size as a whole, i.e. that the great majority of the population migrates past Shark Bay each year. That does not take into account the possibility of sex-biased migration (Brown et al., 1995), nor that in any one year some animals may not migrate as far north up the WA coast as Shark Bay. Given those possibilities, any figure obtained for Group IV population size from aerial surveys off Shark Bay is likely to be a minimum estimate.

## RECENT ANTARCTIC ESTIMATES

Independent estimates of population size and increase rate for the Group IV population have been derived from sightings obtained during the Japanese Research Programme in the Antarctic (JARPA) in Area IV, which includes the Group IV feeding grounds (Matsuoka et al., 2000). Sightings south of 60°S from two sources (dedicated sightings vessels and sighting and sampling vessels) give estimates of abundance in the 1999/2000 Antarctic summer of 12,664 (coefficient of variation = 0.28) and 11,138 (CV = 0.29) respectively. Density estimates from six seasons' data, between 1989/1990 and 1999/2000, give an instantaneous increase rate of 12.41% (Matsuoka et al.: fig. 5), equivalent to an annual rate of 13.2%. It should be noted, however, that there is a small amount of intermingling between animals from each population on the feeding grounds (Chittleborough, 1965; Dawbin 1966), particularly in Area IV to the east of 115°E, so estimates of abundance based on Area IV as a whole (i.e. to 130°E) are likely to be overestimates of the Group IV population.

The Area IV-based population sizes quoted above lie in the upper part of the range calculated for the 1999 Australian west coast survey. In addition to the intermingling already noted, differential migration, where not all animals migrate northward each year, would result in a higher estimate in the Antarctic. Similarly, the increase rate, although within the 95% confidence interval for the Australian west coast estimate ( $10.15 \pm 4.6\%$ ), is higher than the point estimate, and of the order of that recorded recently for animals on the east coast (e.g. Paterson et al., 2001).



### RECENT SOUTHERN HEMISPHERE POPULATION ESTIMATES

Preliminary assessments of Southern Hemisphere population size based on Antarctic catches, adjusted to account for the previously unreported illegal Soviet take and using reported increase rates and target stock sizes (Findlay et al., 2000), place the 1999 Group IV population at 7,686 using the 1977-1991 Australian west coast annual increase rate of 10.9% and 1991 stock size of 3,300 (from Bannister, 1994). The major effect of the greatly increased catches is to increase the estimates of initial population size. Various combinations of catches apportioned between the relevant stocks are used; the above uses the 'Base Case' scenario, with a 'naïve' catch apportionment and no overlap between Groups. For Group IV, rather than the earlier estimate of 12-17,000 (Chittleborough, 1965), initial population size is preliminarily estimated as ~21,000. While the Group IV stock has so far shown encouraging recovery, it is still estimated as some 4,900 (39%) below Maximum Sustainable Yield Level (MSYL, 60% of initial stock size) of 12,600. By contrast, the Group V stock is still considerably depleted, despite a high recent increase rate of 12.3%; the preliminary estimate of 1999 stock size of 4,615 is ~11,500 (71%) below MSYL. The lowest point for either population would have been reached in 1968, with an estimated 268 animals in the Group IV population and 104 in Group V.

### FUTURE AERIAL SURVEYS

Given the disappointing 1999 aerial survey results off Shark Bay, particularly the small number of days' coverage, plans are in hand to undertake another survey in the same area and over the same period as soon as possible. The following considerations will be taken into account.

i) The survey should again have the objective of providing an estimate of absolute abundance of northward migrating animals in the Group IV population.

ii) The former 'box-search' flight path should be replaced by a 'saw-tooth' (zig-zag) format, to provide unbiased, representative, coverage. Legs should extend seawards from the western limit of the bay, i.e. the western shores shore of Bernier, Dorre and Dirk Hartog Is, to allow for migrating animals apparently concentrated close to the coast there (Fig. 3).

iii) To 'ground-truth' the aerial survey sightings, and to provide estimates of swimming speed and diving interval, a program of land-based sightings should be undertaken over at least ten 'good' days from an appropriate location, possibly the southern part of Dirk Hartog Island. This should occur towards the middle of the survey period, i.e. at the expected peak of the migration. It is important that flying and land-based observations occur on the same days.

Timing of surveys beyond the next one should be determined from its results, using a power analysis similar to that undertaken previously (Caputi, in Bannister, 1995) on which the survey planned for three years after 1994 was based. At an annual increase rate of ~10%, 60% initial population level (i.e. 12,600) might be reached very soon: from a 1999 level of 8,000, for example, it would be reached by the year 2002, and from 5,000 by the year 2006. It is clearly important that the next survey should be undertaken as soon as possible.

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# HISTORICAL AND RECENT DISTRIBUTION OF HUMPBACK WHALES IN SHARK BAY, WESTERN AUSTRALIA

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Aerial surveys from 1986 to 1999 indicate a substantial increase in humpback whale (*Megaptera novaeangliae*) numbers in Shark Bay, Western Australia, and provide geographical distribution patterns. A comparison with post World War II catch data (1951-1961) reveals a similar distribution. Bathymetry, water temperature and salinity may influence whale distribution in Shark Bay. Areas of apparent congregation and the correlation with differing boundaries of the Marine Park and World Heritage listed areas are discussed. □ *Humpback whale, Megaptera novaeangliae, Shark Bay, distribution, environment, salinity, sea surface temperature, aerial survey.*

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Humpback whales, *Megaptera novaeangliae*, migrate annually from cold Antarctic Area IV (70°E-130°E) feeding grounds, north along the coastline of Western Australia between May and August to breed in warm tropical waters, and then south between August and December returning to Antarctica. Historically, large numbers of humpback whales were hunted off Western Australia and in the Antarctic Area IV feeding grounds during the mid to late 1930's (Bannister, 1995). Ten years later whaling recommenced at Point Cloates, 250km north of Shark Bay in 1949 and at Carnarvon in 1950 (Fig. 1), with the two operations running concurrently until 1955 when all operations were combined at Carnarvon. They continued there until 1963, resulting in a possible 95% reduction in numbers (from an estimated 12-17,000 individuals to ~800) and an uneconomic basis for further whaling (Chittleborough, 1965).

Recent aerial surveys of Shark Bay and vessel-orientated photographic identification studies in the Dampier Archipelago of northwestern Australia have provided independent population estimates for this Group IV stock of more than 4,000 animals (Bannister, 1991,1994; Jenner & Jenner, 1994) with an annual rate of increase of about 10%. A specific aerial survey was undertaken from June to August 1999 off Shark Bay to estimate this population (Bannister & Burton, 2000; Bannister & Hedley, 2000). A calculated figure of 4,000 animals from this survey is thought to under-estimate the true population. A revised methodology has produced an estimate of between 6,000 and 10,000 humpback whales (Bannister, 2001).

Western Australia has an extensive 12,000km coastline between 12°S and 34°S, 3,000km north of Antarctica. Humpback whale populations move adjacent to the west and northwest sections of coastline, which have several large bays and embayments that are visited during the migration (Jenner et al., 2001). One of the largest of these is Shark Bay, a relatively shallow basin (10-20m) spanning ~8,000sq km of water and separated from the Indian Ocean by three north trending barrier islands, Dirk Hartog, Dorre and Bernier Is (Fig. 1). Shark bay was given World Heritage status in 1991 and has a number of marine protected areas (Fisheries Department of WA, 1994) and a large marine park within its boundary (CALM, 1996) (Fig. 1).

Within Shark Bay, the Peron Peninsula divides the southern half into two semi-enclosed NW-SE elongate gulfs (Fig. 1). These have variable water temperature and salinity regimes (Logan & Cebulski, 1970; Logan & Brown, 1986; Burling, 1998). Water salinity and density increase markedly to the south from the northern oceanic water (Fig. 2A). Low runoff, restricted water circulation and high evaporation promoted by high ambient air temperatures and strong winds are responsible for hypersaline waters at the head of the gulfs, and subsequent maintenance of a number of salinoclines (Bruce, 1997). These two inner gulfs are also characterised by seasonally, highly variable water temperature regimes, with summer having much warmer water and winter much cooler water than the adjacent ocean (Fig. 2B).

The Leeuwin Current, a seasonally varying flow of warm, tropical, low-salinity water 200m

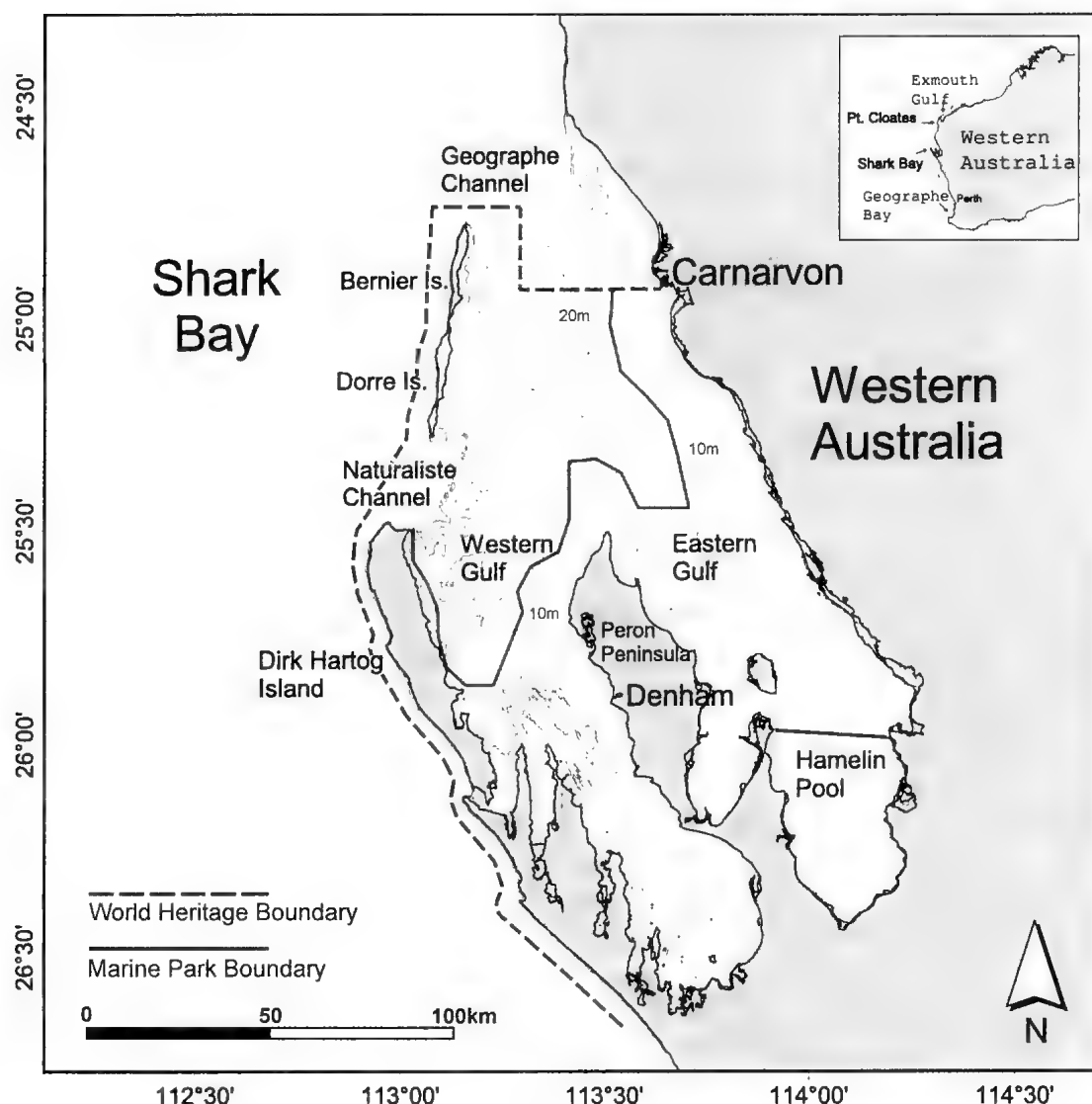


FIG. 1. Map of Shark Bay, Western Australia, showing study area and bathymetry contours.

deep and 100km wide, moves down the Western Australian coast past Shark Bay and into the Great Australian Bight at a speed of between 0.5-1.5m/s. It is strongest between April and October (Pearce & Cresswell, 1985) having an influence on most fisheries and habitats on the west coast (Lenanton et al., 1991; Caputi et al., 1996).

This paper reports on the distribution of humpback whales inside Shark Bay in historical and recent terms. Historically, changes in monthly distribution of catches inside Shark Bay between 1951 and 1961 are considered. In recent

terms the recovery of this population of humpback whales, as demonstrated by aerial surveys conducted since 1976, is considered. Distribution patterns of whales inside Shark Bay are related to environmental parameters, unique to this area.

#### METHODS

*Historical Whaling Catch Data.* Whale chasers operating from Carnarvon were required to keep daily logs. The whaling company also kept detailed records of each whale killed and the amount of oil produced each week. Experienced scientific and technical personnel working at the

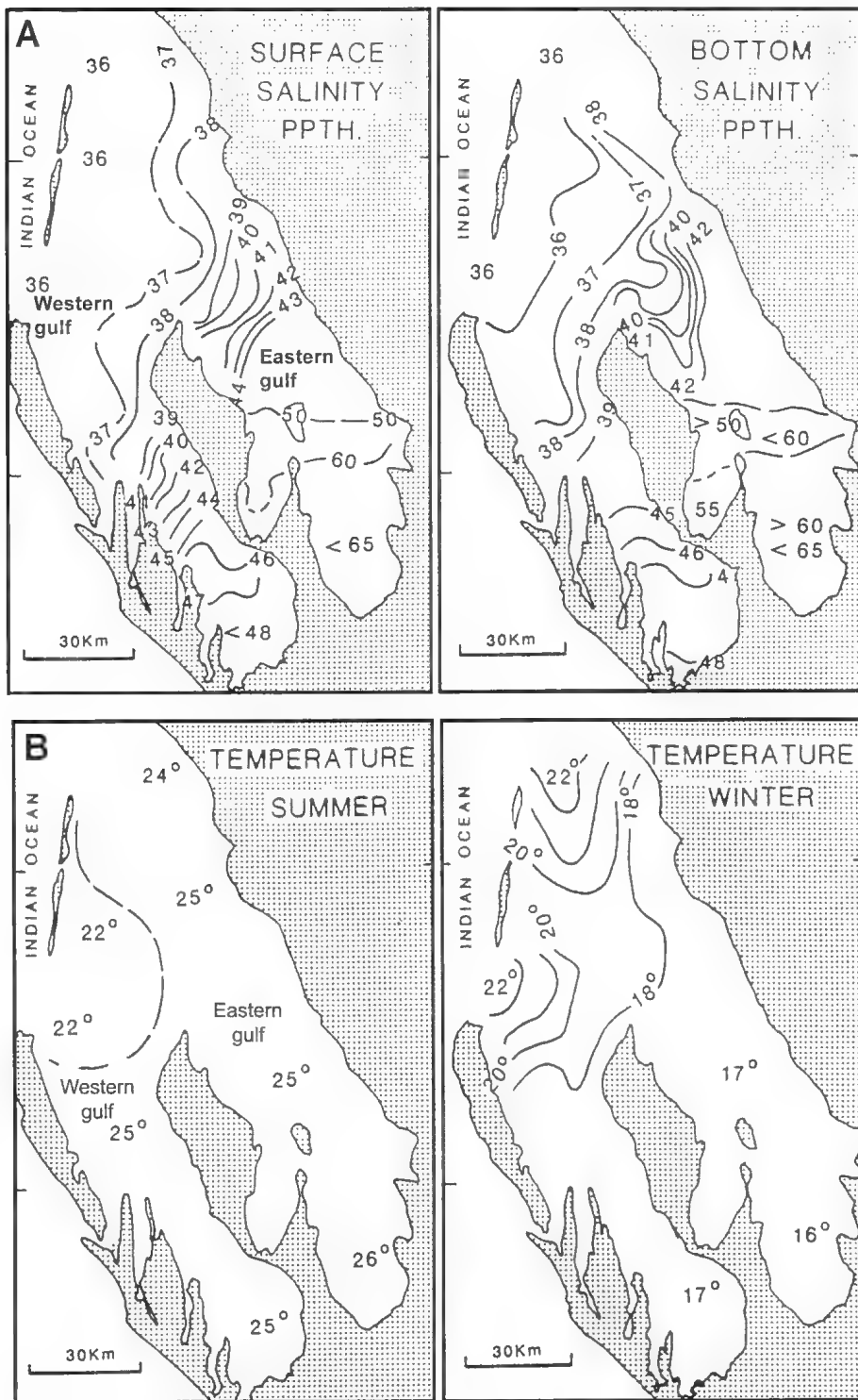


FIG. 2. A, typical patterns of salinity distribution during summer, with strong gradients from ocean passages to the southern extremities of gulfs. B, typical patterns of water temperature distribution for summer and winter (after Logan & Brown, 1986).

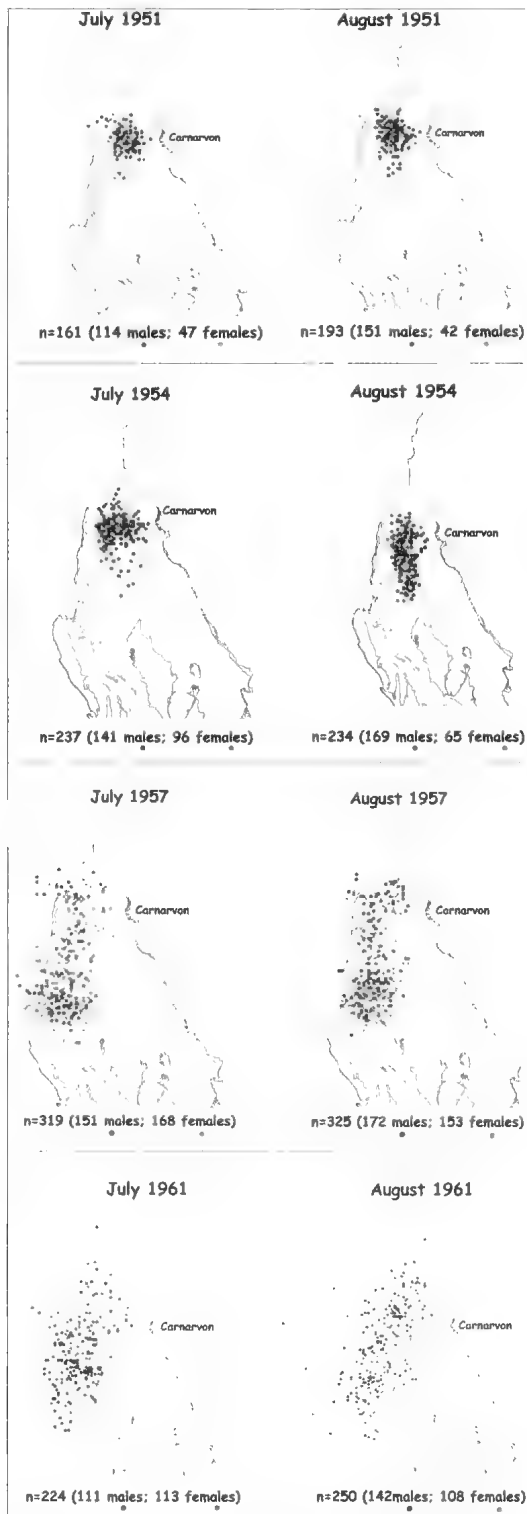


FIG. 3. Plotted positions of humpback whale catches for particular months.

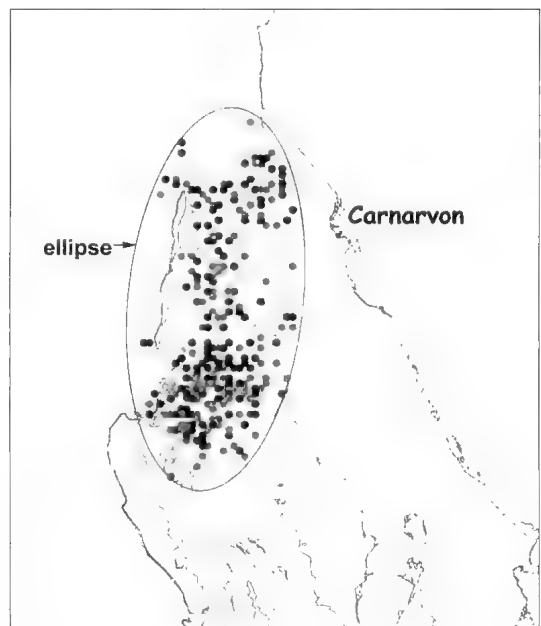


FIG. 4. Delineated area in which humpback whales were caught in Shark Bay (shown for August 1957).

whaling station each winter, sampled as many carcasses as possible (Chittleborough, 1965).

Daily records from four evenly spaced years between 1949 and 1963 were entered into a database. The positions (latitude and longitude) of animals killed during June, July, August and September of 1951, 1954, 1957 and 1961 were plotted onto outlines of Shark Bay using 'Arcview GIS' software. Of these months, only July and August are represented in all four years (Fig. 3), and are used to investigate the changes in monthly distribution during this period of intensive whaling effort.

An index of whale (catch) density was calculated by approximating the area covered by whale chasers for each year and dividing it by the number of whales killed in that area. An ellipse was drawn over each monthly plot of whales caught so that all catch positions were inside the perimeter, and the area calculated with 'NIH Image' software, using a standard calibrated distance (Fig. 4).

*Recent Aerial Surveys.* To estimate relative abundance of humpback whales migrating along Western Australia's coast, a series of aerial surveys have been conducted approximately every 3 years since 1976 up to 1994, following a consistent pre-determined flight path outside Shark Bay (Bannister, 1994) (Fig. 5). These surveys were conducted with an experienced



pilot/observer and one observer in a high wing Cessna 337 aircraft. For the purpose of this paper, individual sighting locations of humpback whales observed from the three transit legs inside Shark Bay during the aerial surveys conducted in 1986, 1988, 1991 and 1994 are used to estimate the latitude and longitude for each whale. Cumulative numbers of humpback whales observed on the transit legs over a similar 10-day period in July in each of these years are presented in Fig. 6.

In 1999, a comprehensive aerial survey was undertaken on the northern migration outside Shark Bay (Bannister & Burton, 2000; Bannister & Hadley, 2000). Observations made on the three transit legs inside Shark Bay were comparable to the earlier flights and are used in this study (Fig. 6). In addition to this survey, which extended from late June to mid August 1999, six flights were conducted inside Shark Bay between July 5 and August 16, using a grid that effectively covered the areas where whales had been sighted during previous surveys, and where humpback whales were taken during whaling (Fig. 7). This survey was conducted to collect whale distribution data in Shark Bay rather than abundance.

A twin engine Partenavia high-wing aircraft with two dedicated observers was used at 1500ft and 120 knots ground speed. The aircraft was fitted with bubble windows on either side. Numbers of whales and pods, directions of movement, behaviour and accurate GPS positions were logged. Angles of declination were measured using a clinometer. The perpendicular distance of each sighting from the aircraft was calculated using the angle of declination to each sighting and the height of 457m above sea level. Distances from the port and starboard sides of the aircraft were then converted into proportions of latitudes and longitude for plotting in Arcview. Transects were between 7 and 8 nautical miles (nm) apart to minimise duplicate sightings.

#### STUDY AREA

Studies of the geology and oceanography of Shark Bay (Logan & Cebulski, 1970; Logan & Brown, 1986) indicate a semi-arid climate with a diverse range of habitats including arid surrounding lands, extensive seagrass banks of *Amphibolis antarctica*, *Posidonia australis* and *Halodule uninervis* (Walker, 1989), coral reefs, shallow sand areas and deep water muds. The water body is reasonably well mixed vertically but varies spatially. The marine environment is characterised by a diverse range of hydrographic

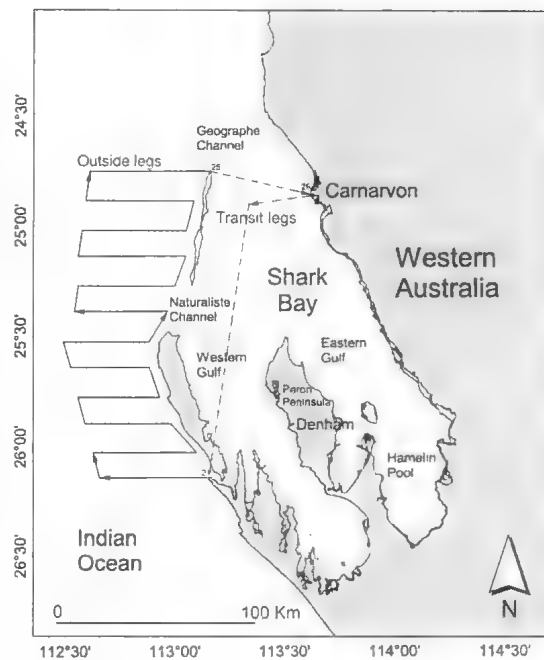


FIG. 5. Flight path for aerial surveys conducted outside Shark Bay during July between 1976 and 1999.

features including seasonally variable water temperatures (15–30°C) and broad salinity gradients (35–65ppt) in the two gulfs within the bay (Fig. 2). The water mass in Shark Bay is divided into three main categories (Logan & Cebulski, 1970) based on characteristic salinity and density values: oceanic (35–40ppt), meta-haline (40–56ppt) and hypersaline (56–70ppt) (Fig. 8). Boundaries of these water masses are located at salinoclines, where the salinity gradient is steep. The large Cape Peron salinocline delineates inner gulf waters from oceanic water (Fig. 8) remaining a permanent feature in summer, but less strongly developed in winter (Logan & Cebulski, 1970). Water temperatures and salinity values north and west of this feature approximate those of oceanic waters entering from the adjacent continental shelf through both Geographe and Naturaliste Channels (Logan & Cebulski, 1970; Logan & Brown, 1986; Burling, 1998).

*Remotely Sensed Images.* To observe the variation in water temperatures in Shark Bay on a broad scale, remotely sensed images of sea surface temperature (SST) derived from the Advanced Very High Resolution Radiometer (AVHRR) instrument aboard the NOAA satellite were acquired from CSIRO marine laboratories in Western Australia, corresponding to the date

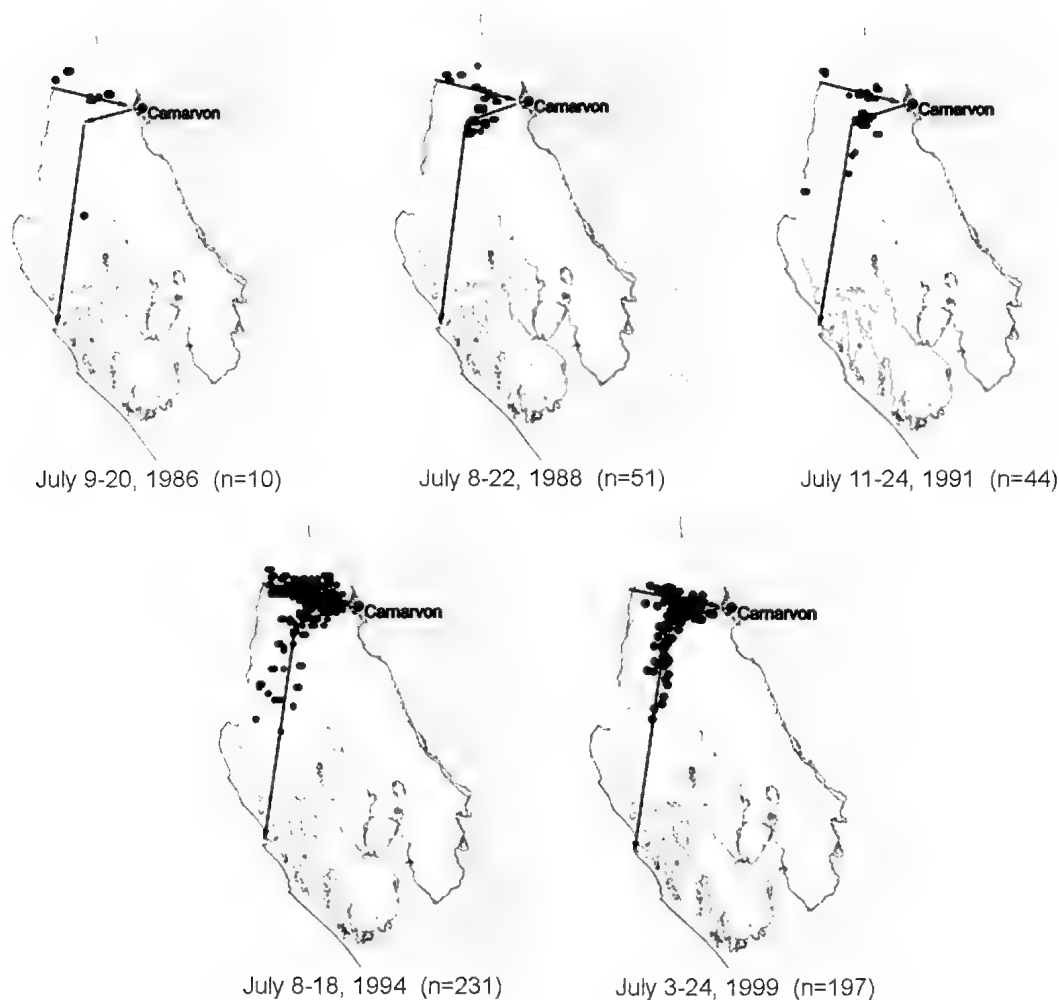


FIG. 6. Plotted positions of whales sighted on the 'inside legs' of flight path for aerial surveys conducted between 1986 and 1999.

closest to each flight of the survey. Observations of whale sightings made during the aerial survey in 1999 (flights 1,2,5 and 6) are overlaid onto these calibrated SST images and bathymetry, using 'Arcview GIS' software (Fig. 9).

### RESULTS

**HISTORICAL.** Plots of humpback whale catches in Shark Bay for four years between 1951 and 1961 show large differences in distribution and density of catches. Distributions of catches in July and August of 1951 and 1954 are similar (Fig. 3) with catches concentrated in the central northern part of the Bay, just west of Carnarvon. By 1957, the catch distribution was spread over a much larger area within Shark Bay, extending south into the western gulf. Most whales were

caught outside Shark Bay in 1961, with fewer catches made inside Shark Bay (Fig. 3).

Density of whale catches decreased dramatically between 1954 and 1957, as the area searched by the chasers increased from approximately 4,000sq nm to over 6,000sq nm (Fig.10A). By 1961 the search area had increased to over 12,000sq nm. The crude index of catch density reflects this situation with a dramatic fall from 0.23 whales per square nm in 1951 to 0.05 in 1961 (Fig. 10B). Whales were killed predominantly in the northern central areas close to the whaling station up to 1954, extending to the lower areas of the Bay into the western gulf from 1957 (Fig. 3). No whales were taken from the eastern gulf during the four years of data sampled for this work.

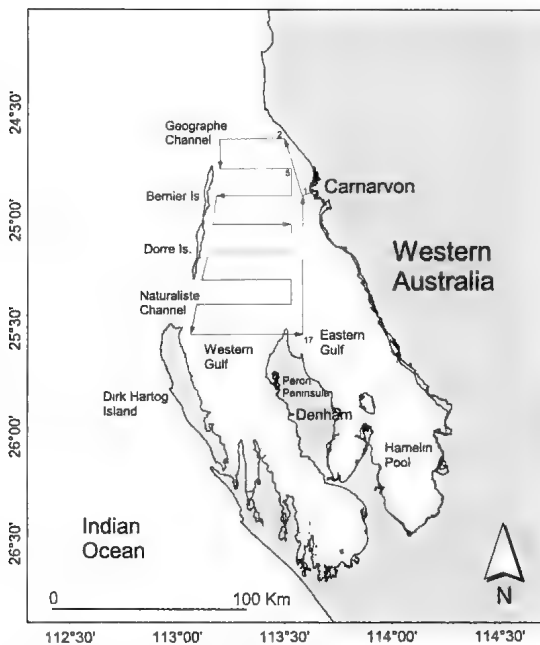


FIG. 7. Flight path for aerial surveys conducted inside Shark Bay during July and August of 1999.

**RECENT: AERIAL SURVEYS.** Plotted whale sighting data from the three transit legs of the aerial surveys in July 1994 and 1999 show higher numbers of humpback whales than in 1986, 1988 and 1991 (Fig. 6). For the combined 10-day survey periods of each year, these figures indicate a relative increase in the number of whales in the northern area close to Carnarvon. In 1994 and 1999 more whales were observed further south in central Shark Bay.

In 1999 the six surveys flown on the dedicated grid pattern inside Shark Bay (Fig. 7) indicate a much broader distribution (Fig. 9) than those sightings taken from the three transects of the bay on the standard grid pattern (Fig. 6), due mainly to the increased number or survey legs. The effective area surveyed per flight was approximately 1600sq nm with a total transect distance of 280nm. Details of each completed flight are shown in Table 1. The total number of whales sighted was 310 comprising 302 (97.4%) humpback whales (including 18 probable), 2 probable southern right whales and 6 unidentified whales. Average flight time was 2.5hrs (se = 0.088) and the mean number of humpback whales sighted per hour was 19.5 (se = 4.1). The total hours of flying were adjusted by -0.1hrs to remove the time taken to move to and from the first and last waypoint. The number of whales observed inside

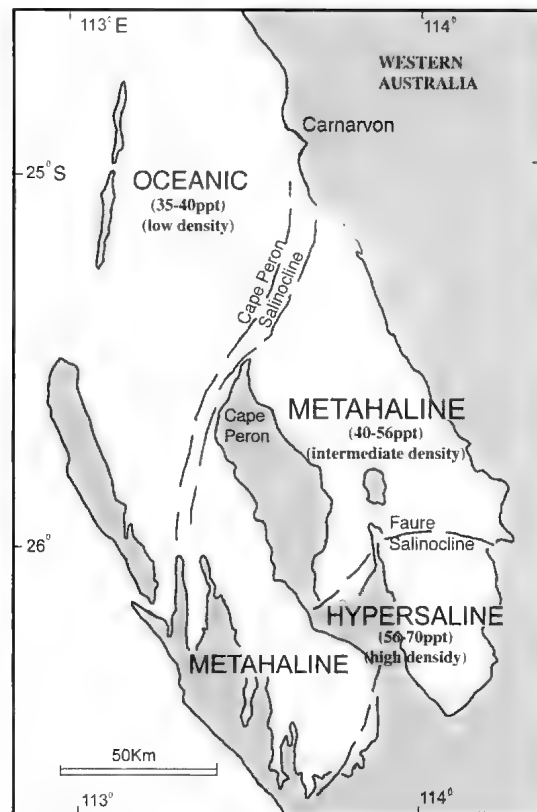


FIG. 8. Three bodies of water in Shark Bay (after Logan & Cebulski, 1970).

Shark Bay continued to increase into August as those observed outside the Bay began to decrease (Fig. 11A). The number of humpback whales sighted/adjusted hour steadily increased from 7.5 on July 5 to 37.2 on August 16 (Fig. 11B). Between 93 and 98% of sightings were within 4.5-7km from the trackline respectively (Fig. 12).

In early July (flights 1 and 2, Fig. 9), humpback whales were found within Shark Bay, predominantly in the northern sector. By August (flights 5 and 6, Fig. 9), large numbers of humpback whales were more evenly distributed, in both deep and shallow areas, extending from west of Carnarvon, south to the northern opening of the western gulf. Most whales were observed in areas of water temperatures of 20°C or warmer and west of a line from Cape Peron to Carnarvon. Few sightings were made in the eastern part of the survey area.

## DISCUSSION

Extensive research undertaken on this Group IV population of humpback whales and on the

TABLE 1. Shark Bay humpback whale aerial survey June-August 1999. Summary of completed 'inside' flights.

Flight date	HB	HB?	Total HB	Other whales	Flying hours	Adjusted hours(-0.1)	HB/Hour
5-Jul-99	19	0	19	0	2.6	2.5	7.6
12-Jul-99	35	0	35	2	2.5	2.4	14.58
23-Jul-99	52	3	55	0	2.6	2.5	22.00
31-Jul-99	31	7	38	1	2.6	2.5	15.2
10-Aug-99	55	7	62	4	3.1	3	20.67
16-Aug-99	92	1	93	1	2.6	2.5	37.2
Total	284	18	302	8	16	15.4	

Group V population along the east coast of Australia during the 1950's, documented their decline during commercial whaling operations and added considerably to knowledge of their biology (Chittleborough, 1965). During 14 years of whaling on the West Australian coast, over 12,000 animals were killed. At Carnarvon, quotas were allocated each year and varied when the operations from Point Cloates were combined with those in Shark Bay and when catches began to decline in 1958.

In Western Australia during the early 1950's many humpback whales could be found inside Shark Bay. The catch distribution did not reflect the actual distribution of animals in the area, as whale chasers could locate whales close to their base at Carnarvon. As the population declined from the late 1950's the density of whales decreased and whalers had to increase their search effort to a much wider area and employ the use of spotter aircraft to maintain catches (Chittleborough, 1965). This is evident with the distribution of catches in 1957 (Fig. 3) which shows a much wider spread, predominantly south into the north of the western gulf. No humpback whales were caught in the eastern gulf of Shark Bay during these years. The eastern gulf was rarely searched as few whales were expected there, and no whales were observed in the western gulf during transit to Denham while undertaking a marking program (Chittleborough, pers. comm.). No literature is available describing the presence of whales in the eastern gulf. By 1961, chasers had to travel predominantly outside Shark Bay to find whales, as densities inside had dramatically decreased.

It could be inferred from the change in catch distributions from 1951 to 1961 that the density of whales in the early 1950's would have been high throughout the northern sector of Shark Bay, down to the western gulf, even though whales were only caught close to Carnarvon. Whalers

did not have to search a large area. However, the distribution inside Shark Bay seemed confined to an area west of a line from Carnarvon to Peron Peninsula, and half way down the western gulf.

Aerial surveys from the late 1970's conducted outside Shark Bay during the northern migration in July show a major population increase since 1982 (Bannister, 1991, 1994). The most recent surveys (1994, 1999) strongly suggest that as the population has increased, so the proportion of whales found inside the bay (39.7% and 27.3% of total sightings respectively) is also increasing, although less so in 1999 (Fig. 11) (Bannister, 1994; Bannister & Burton, 2000). The increase in proportion observed inside the Bay (from 15.4% to 39.7%) in 1991 and 1994 respectively, seems abnormally high given the time difference of three years between these surveys. An explanation for the apparent inter-annual differences in whale numbers inside Shark Bay may be that the peak in migration could have been missed in 1991 and therefore fewer whales were present during the time of the survey. Variability in timing of the peak of the northern migration may be up to three weeks, possibly influenced by the availability of food in the Antarctic (Chittleborough, 1965).

Reasons why whales are observed inside Shark Bay are unclear. There are no data that define the residence times of animals which visit the bay, as only limited photo-id work has been carried out here (Table 2) with six pods observed over four days of effort during 1999. Of 15 humpback whales identified from 1985 to 1989 in Shark Bay by the author, one animal was photographed on 12 July 1989, then observed twice 10 weeks later off Perth, 800km south, in September (Burton, 1991). The factor of site selection or specificity by individuals or certain proportions of the population could play a role here: i.e. particular individuals may travel to particular areas of the Western Australian coast and remain there,

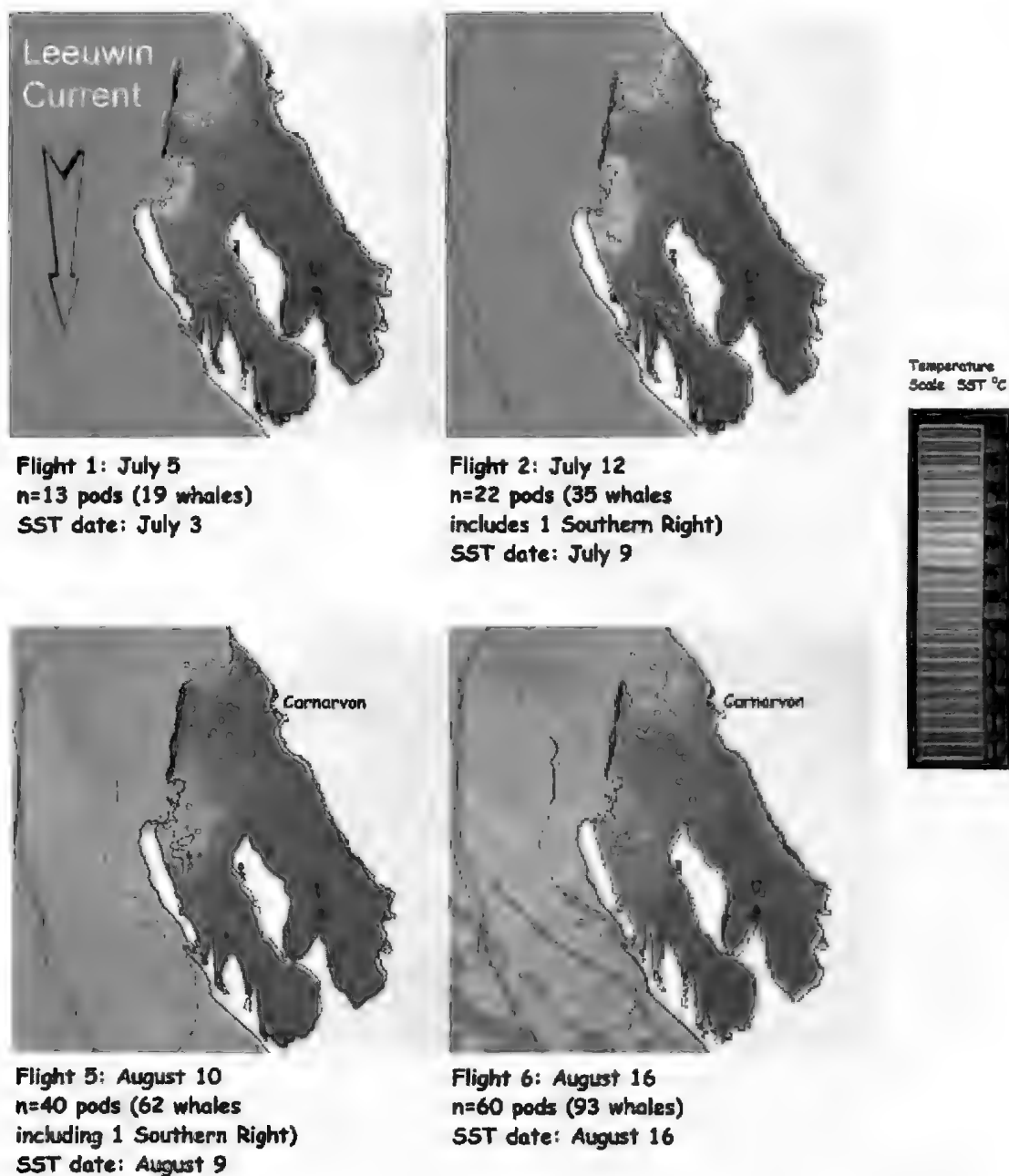


FIG. 9. Whale sightings overlaid onto SST images during 4 of the 6 flights conducted inside Shark Bay in 1999.

without traversing the whole coastline during the migration. It is quite likely that a proportion of this population may spend some time in Shark Bay, as individuals have been observed in waters off Perth from between four and seven days (Burton, 1991). Further matching of photographs from a recently developed computer assisted

database may provide other resights along the Western Australian coast (Elford, pers. comm.) and assist with answering several of these questions.

During the northern migration, humpback whales enter Shark Bay through both major

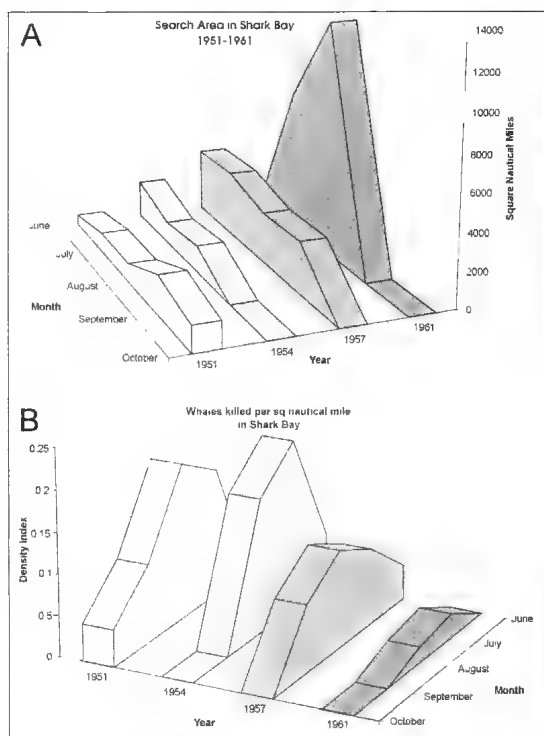


FIG. 10. Quantitative description of the search area (A) for each of the 4 years and a density index (B) of whales killed within those areas.

entrances, Naturaliste and Geographe Channels (Fig. 1). Shark Bay may be an important resting area for the north-bound whales as they would be swimming against a strong south-flowing Leeuwin current (Pearce & Cresswell, 1985). Outside Shark Bay the majority of north-bound whales are within 10-15nm from the coast (Bannister & Burton, 2000). Only a small proportion were observed further offshore, possibly explained by the fact that the strongest flow of the Leeuwin Current is southward along the continental shelf during autumn to spring (Pearce & Cresswell, 1985), i.e. approximately 30-50nm outside Shark Bay. During the southern migration, whales would probably enter Shark Bay through Geographe Channel, as it is a natural opening to the migration corridor from the north.

A comparison of the directional movement of humpback whales observed during the outside legs and inside bay flights in 1999 indicates a lower proportion of animals moving north (9%) inside the bay compared to outside (44%), and a higher proportion moving in all other directions (Table 3). Although these data represent a 'snapshot' of behaviours in time during the

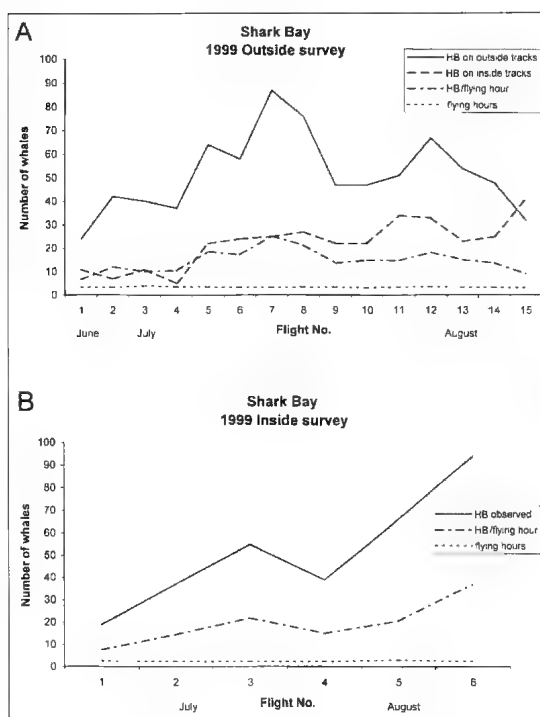


FIG. 11. Whales sighted during aerial surveys in 1999 outside (A) and inside Shark Bay (B).

northern migration, they do indicate that there is less northward movement by those animals inside Shark Bay, and that there is reason to believe that some animals are resting or milling there.

Satellite derived sea surface temperature (SST) images show the interaction of the Leeuwin Current with surrounding water masses (Prata et al., 1989) (Fig. 9). It appears that the direct influence of the Leeuwin Current is restricted to the northern regions of Shark Bay, with little effect on the eastern and western gulfs (Burling, 1998). The intrusions of oceanic water into the

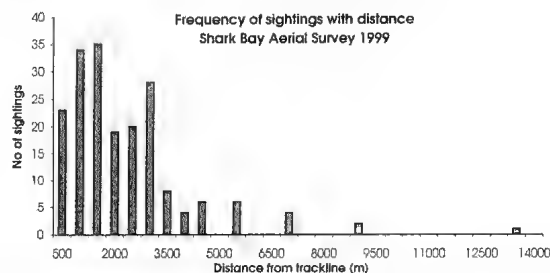


FIG. 12. Frequencies of whales sighted at various distances from the aircraft, 1999.

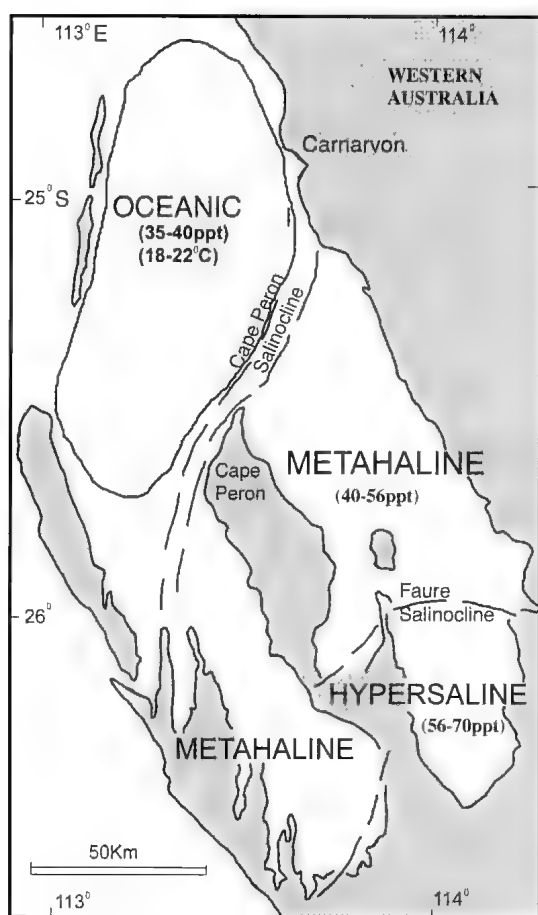


FIG. 13. Distribution of humpback whales in relation to the winter oceanic regime inside Shark Bay.

Bay as observed in the SST images (Fig. 9) appear to be tidally driven, and are augmented by persistent southerly winds. Large scale exchange of bay water with oceanic water seems to be restricted to winter months (Burling, 1998).

The number of humpback whales inside Shark Bay steadily increases from June to August as the peak of the northward migration passes in July, and southerly migrating animals begin appearing (Figs 3, 9). Densities increase within Shark Bay and distribution expands through the central and western parts with observations until early November, based on recent whale-watching data. No whales were caught in the eastern gulf area nor were any observed there during aerial surveys in 1999. Strip-transect aerial surveys conducted in Shark Bay in July 1989 and June 1994 for estimates of dugong (*Dugong dugon*) abundance also found relatively few humpback

TABLE 2. Photo-id data collected inside Shark Bay, June and July 1999. ad = adult, sad = sub-adult, fl = fluke, ld = left dorsal, rd = right dorsal.

Date	Pod details	Photo-id details	Individual id
26/6/1999	Pod 1 2ad 1sad	fl1 ld1, rd2	2
27/6/1999	Pod 1+2 3ad 1sad	fF11-3	3
	Pod 3 1 Bryde's whale	rd	1
11/7/1999	Pod 1 2ad	ld1	1
	Pod 2 2ad	fl1	1
20/7/1999	Pod 1 cow/calf	rd cow, rd calf	2

whales (Preen et al., 1997). During these surveys, the majority of humpback whales (13 of 14 in 1994 and all 6 in 1989) were found in the northern and western areas of the bay and it was thought that their distribution was restricted to the oceanic waters there. An aerial survey to estimate dugong abundance during July 1999 also found few humpback whales, with none sighted in the eastern gulf (Gales & McCauley, pers. comm.).

Distribution of whales inside Shark Bay may be related to unique environmental conditions such as water temperature, salinity and bathymetry. The inner, southern areas of Shark Bay are shallower, more saline and exhibit large seasonal variations in water temperature (Logan & Cebulski, 1970). The Cape Peron salinocline (Fig. 13) may present a natural barrier to the movement of whales down the eastern gulf, where salinity increases markedly and water temperatures are lower than the oceanic waters north of Cape Peron during winter.

There have been no recorded observations of humpback whales feeding in Shark Bay. No food remains were reported in stomachs of humpback

TABLE 3. Proportions of humpback whales moving in the compass rose directions, from the aerial surveys outside and inside Shark Bay 1999.

Direction component	Outside flights (n whales =773)	Inside flights (n whales =302)
North	43.9%	8.94%
Northeast	5.82 %	6.62%
Northwest	0.26 %	7.95 %
South	5.69 %	8.29 %
Southeast	0.39 %	6.95 %
Southwest	0.78 %	2.65 %
East	0.91 %	2.32 %
West	1.04 %	3.64 %
Other	41.27 %	52.65 %
Total	100%	100%



whales sampled at Carnarvon (Chittleborough, 1965). The zooplankton of the area was shown to be abundant in the central part of the bay, decreasing by four orders of magnitude to the southern hypersaline gulfs (Kimmerer et al., 1985). Other whale species have been recorded inside Shark Bay, the author observing a Bryde's whale feeding on small pelagic fish, 5 miles to the north of Cape Peron in 1998 and another Bryde's whale in the northern sector during vessel-based photo-identification trips in 1999 (Table 2).

North of Shark Bay along Ningaloo Reef, small amounts of zooplankton including *Euphasia hemigibba* and *Pseudeuphausia latifrons*, were found in the stomachs of 5 humpback whales examined during whaling from Point Cloates (Fig. 1), (Chittleborough, 1965). Recent work off Ningaloo Reef has discovered inter-annual summer variation in macrozooplankton, including *P. latifrons*, that relate to gross changes in oceanographic conditions (S. Wilson, pers. comm.). Wilson et al. (2001) describes the daytime swarming behaviour of *P. latifrons* off Ningaloo in relation to feeding by manta rays and whale sharks. A recent sighting of a blue whale feeding in waters off the Ningaloo continental shelf area was made during an aerial survey for humpback whales (C. Jenner, pers. comm.).

It is expected that the recovering Group IV population of humpback whales will increasingly use Shark Bay. Whales are observed in the northern and western areas of the bay where oceanic conditions predominate (Fig. 13). They seldom venture further south into the bay possibly because oceanic water is restricted from moving into these gulfs by the complex hydrographic regime of salinoclines associated with hypersaline water. It is noteworthy that the state Marine Park boundary almost totally excludes the area in which the majority of humpback whales congregate during migration (Fig. 1).

Further work in Shark Bay should include boat-based photo-identification studies for determining residence times and to provide an understanding of social interactions and behaviour of humpback whales, as well as monitoring environmental and man-made influences on the area.

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**AN ECONOMIC JUSTIFICATION FOR THE CONTINUED PROTECTION OF WHALES IN TONGA. (POSTER)** Tongans utilised whales as a source of food until 1978 when whaling was banned by Royal Decree. In August of 1999, concurrent with a visit by representatives from the pro-whaling group the World Council of Whalers (WCW), a female humpback whale was killed and butchered near Nuku'oalofa, the Kingdom's capital. Meat from this whale was sold for local consumption. There is, therefore, with the explicit support from the WCW, a move to resume whaling in the Kingdom of Tonga and the issue is being considered within both the Tongan government and the Royal Family. However, there is a growing whale watching industry in Tonga. Thus, it is important to assess the economic impacts of whale based tourism in these islands and to consider the potential effect of a resumption of whaling on this tourism industry. A study was conducted in August 1999 to provide a preliminary assessment of the economic benefits of whale watching for the Vava'u island group. Results show that 78% (900) of air holiday-makers went whale watching and about half (400) of yacht visitors watched whales, contributing between T\$78,000 and T\$116,000 in direct expenditure on whale watching in Vava'u each season. Those visitors to Vava'u who came specifically to watch whales (an estimated 378 people) spent an additional T\$567,847 on accommodation,

food, transport, souvenirs and other items whilst in Vava'u. The five permitted whale watch operators in Vava'u spent an estimated T\$54,464 on their whale watch operations and employees of those whale watch businesses spent an additional T\$44,000 in Vava'u each season. Consequently, the 'use' value (the direct, indirect and induced expenditure) of whales as a tourism resource is estimated to be between T\$746,000 and T\$784,000 each year. The true multiplier effect of whale tourists' expenditure in the Vava'u community would exceed T\$1,000,000 each year. Respondents were also asked to consider whether the hunting of whales in Tonga would reduce their likelihood of visiting. 65% of yacht visitors and 73% of air holiday-makers agreed that they would be less likely to visit Vava'u if whales were hunted there. Thus, any change in the protective status of whales and resumption of whaling practices would likely displace a large proportion of the 'whale tourists' to Tonga. There is, therefore, a likely 'opportunity cost' with regard to any lethal use of the whales. It appears unlikely that a whale watching industry could co-exist with a lethal use of whales in Tonga.

Mark B. Orams, Centre for Tourism Research, Massey University at Albany, Private Bag 102 904, North Shore MSC, New Zealand; 29 August 2000.

**HUMPBACK WHALES IN FRENCH POLYNESIA. 1988-1999. (ABSTRACT)** From 1988-99, humpback whales (*Megaptera novaeangliae*) were sighted from 15 June - 24 November near 25 of French Polynesia's islands. At seven islands, whales entered enclosed lagoons by swimming through reef passes, venturing over 5km from the sea. Nursing calves were observed; three stranded at three islands. From 1991-99 shore and boat surveys were conducted on humpback whales at Moorea in the Society Islands, and in 1999 at Rurutu in the Austral Islands. Whales were photographically identified; social groups and behavior documented; sloughed skin collected from 19 groups; and songs recorded. Cow/calf pairs were sometimes accompanied by escorts. Male competitive behaviour was observed only 50-200m off Moorea's barrier reef; some whales then entered the lagoon through 8 reef passes, venturing 3km from the sea for 20 minutes to over 48 hours; cow/calf pairs remained in the lagoon longer than other whales. From 1992-99, 110

individual whale flukes were identified at Moorea; 17 additional individuals were identified at Rurutu. Repeat sightings of whales were made within single seasons, but only six individuals were observed two or more years. Similar results were obtained from analyses of dorsal fins. In 1998 one whale was observed at Moorea and also at Palmerston Atoll, Cook Islands. A possible three-site match exists for a female at American Samoa (1994, with calf), Moorea (1996) and Rurutu (1998, with calf). French Polynesia is a breeding ground for whales that are most likely part of Antarctica's Area VI stock, and some movement to and from other breeding grounds occurs.

Michael Poole, Marine Mammal Research Program, Centre de Recherches Insulaires et Observatoire de l'Environnement (CRIOBE), B.P. 1013, Papeetoi, Moorea 98728, French Polynesia (e-mail: criobe@mail.pf); 29 August 2000.

**CONSISTENT HABITAT PREFERENCES OF INDIVIDUAL HUMPBAC WHALES WITHIN THE GULF OF MAINE. (ABSTRACT)** The Gulf of Maine is one of six, relatively discrete feeding grounds of the North Atlantic humpback whale (*Megaptera novaeangliae*). While individuals have been shown to move extensively within its boundaries, there is also evidence that habitat preferences can restrict the movement and exchange of individuals. Segregation within the Gulf of Maine was examined using the sighting histories of 1,170 catalogued individuals. The majority of the sightings were made on Stellwagen Bank, where photo-identification data were collected from commercial whale watching platforms on a daily basis during the summer season (June 1-September 30), 1979-1998. Sightings were also obtained during 13 annual research cruises that targeted humpback whale habitats. Despite a strong observer bias on Stellwagen Bank, 50% (n=586) of the

catalogued population was never sighted there during the summer season. Even in an immediately adjacent habitat, the Great South Channel, 26% (n=118) of the individuals sampled had no Stellwagen Bank sighting history. By contrast, 7% (n=77) of Gulf of Maine whales exhibited a preference for Stellwagen, having been sighted there in more than half of their catalogued years. The highest annual return was exhibited by an individual that was re-sighted on Stellwagen Bank in 18 of 20 catalogued years. Non-random movement and segregation within a feeding ground has the potential to bias the measurement of population parameters, such as abundance estimates based on mark-recapture data.

Jooke Robbins (e-mail: jrobbins@coastalstudies.org) and David K. Mattila, Center for Coastal Studies, PO Box 1036, Provincetown, Massachusetts 02657, USA; 29 August 2000.

# DISSECTION OF A HUMPBACK WHALE CALF LARYNX WITH PARTICULAR REFERENCE TO THE RELATIONSHIPS OF THE VENTRAL DIVERTICULUM

C.J. QUAYLE

Quayle, C.J. 2001 12 31: Dissection of a humpback whale calf larynx with particular reference to the relationships of the ventral diverticulum. *Memoirs of the Queensland Museum* 47(2): 613-616. Brisbane. ISSN 0079-8835.

The larynx of a humpback whale calf was sectioned transversely and orientated with a specimen of similar size which had been sectioned longitudinally (Quayle, 1991). The relationships of the ventral diverticulum (or sac) and its histological appearances are described as well as possible function of this structure which is unique to baleen whales. □ *Humpback whale, Megaptera novaeangliae, larynx, ventral diverticulum, relationships and possible function.*

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The ventral laryngeal diverticulum (or sac), unique to baleen whales, was first described in a piked whale (= minke whale, *Balaenoptera acutorostrata*) by Hunter (1787) who presumed that whales did not produce sound as they lacked vocal cords. Payne & McVay (1971) established that humpback whales (*Megaptera novaeangliae*) produce elaborate sounds in the form of song but the means of production remain speculative. Hosokawa (1950) reviewed the literature, concerning the anatomy and possible function of the diverticulum, published in the two centuries following Hunter's observations and contributed substantially to that knowledge principally by detailed dissection of an adult sei whale (*Balaenoptera borealis*) larynx.

Opportunities to dissect baleen whale larynges in Queensland have been limited to neonatal and sub-adult specimens (Quayle, 1991; Paterson, 1994; Paterson et al., 1993) with the exception of one adult *B. acutorostrata* (Paterson et al., 2000). A further humpback whale calf laryngeal dissection is described in this paper.

## MATERIAL AND METHODS

A 3.6m long female humpback whale calf, with umbilical cord attached, was found dead at Dundubara (25°10'S, 153°17'E) on the eastern shore of Fraser Island on 26 July 1999. The larynx was removed in a fresh state, frozen immediately, transported to the Queensland Museum and registered QMJM13647.

The larynx was subsequently thawed and sectioned serially in the transverse plane. Five of those sections are described, commencing with the most caudal, with reference to a longitudinal section (Fig. 1) of a male humpback whale calf larynx (Quayle, 1991).

The tracheal lumen, fundus of the ventral diverticulum and the oesophageal lumen are shown in section I (Fig. 2). Minimal invagination of the tracheal lumen by the diverticulum is evident. In section II (Fig. 2) the diverticulum 'extends' into the lumen via the ventral deficiency in the tracheal cartilages. The oesophagus is dorsal to the trachea. In section III (Fig. 2), made at the caudal margin of the interarytenoid bar (or fibro-elastic connection), the thick walled diverticulum reduces the tracheal lumen to a crescentic slit. The diverticular lumen is small. The oesophagus, with thick musculature at that level, is again seen dorsally. In section IV (Fig. 2), made at the mid cricoid level, the paired arytenoid bodies are seen. In life, the air stream would pass between their medial surfaces to enter (or exit) the trachea or diverticulum. A groove between the ventral aspects of the arytenoids leads into the neck of the diverticulum which is narrowest ventral to the interarytenoid bar. Section V (Fig. 2), the most cephalad section, was obliquely cut with resultant 'displacement' of the cricoid to the right of the figure. The paired arytenoids are again demonstrated. The wide ventral passage leads to the neck of the diverticulum.

Histological examination of the diverticulum demonstrated that its mucosal surface comprised non-ciliated, pseudo-stratified epithelial cells with abundant mucous secreting glands in the submucosa (Fig. 3A,B). The underlying muscle was striated and typical of voluntary (skeletal) muscle (Fig. 3C). Other sections, although not illustrated here, demonstrated that the muscular bands were often disposed both circumferentially and longitudinally.

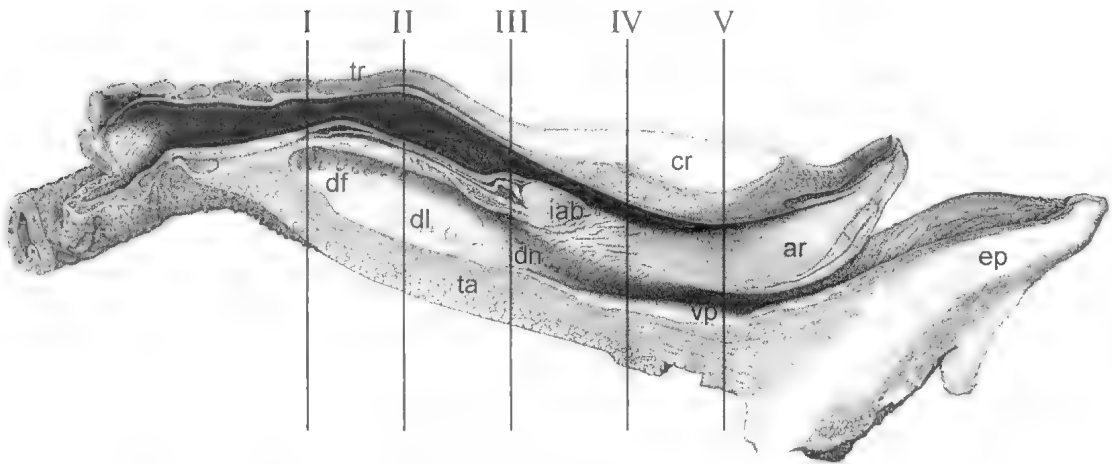


FIG. 1. Positions from which transverse sections of QMJM13647 were cut. They are orientated with a longitudinal section in medial aspect of a humpback whale calf larynx, Quayle (1991). The tracheal lumen in that specimen widened following formalin fixation. ar = arytenoid cartilage; cr = cricoid cartilage; df = fundus of diverticulum; dl = lumen of diverticulum; dn = neck of diverticulum; ep = epiglottic cartilage; iab = inter-arytenoid bar; ta = thyro-arytenoid muscle; tr = trachea; vp = ventral air passage.

The diverticulum was 10cm long with a relatively small lumen and an extremely thick muscular wall. It was probably non-distensible (at least in this neonate). Its contents (air and/or water) could be expelled into the larynx proper between the bodies of the arytenoids. However, if they were apposed, thus closing the entrance to the diverticulum (Paterson, 1994, fig. 1

demonstrated the narrow diverticular entrance in *B. acutorostrata*), the diverticulum may 'round-up' on contraction and reduce the tracheal lumen from its ventral aspect. Simultaneous contraction of surrounding muscles (thyro-arytenoid in particular) could assist in maintaining the diverticulum in that position.

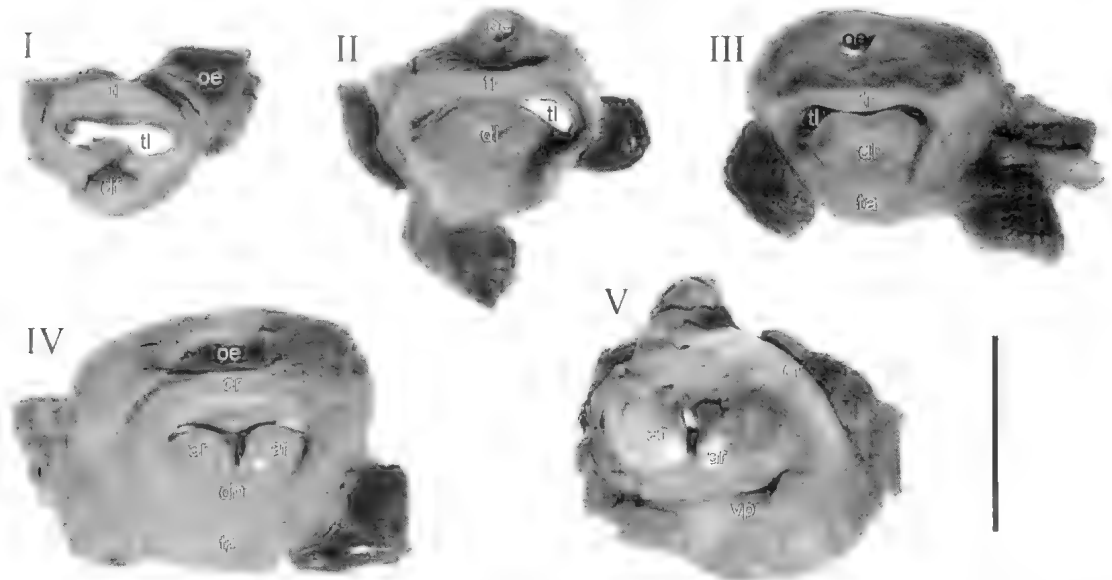


FIG. 2. Transverse laryngeal sections I-V of QMJM13647. ar = arytenoid cartilages; cr = cricoid cartilage; df = fundus of diverticulum; dl = lumen of diverticulum; dn = neck of diverticulum; oe = oesophagus; ta = thyro-arytenoid muscle; tl = tracheal lumen; tr = trachea; vp = ventral air passage. Scale bar = 10cm.

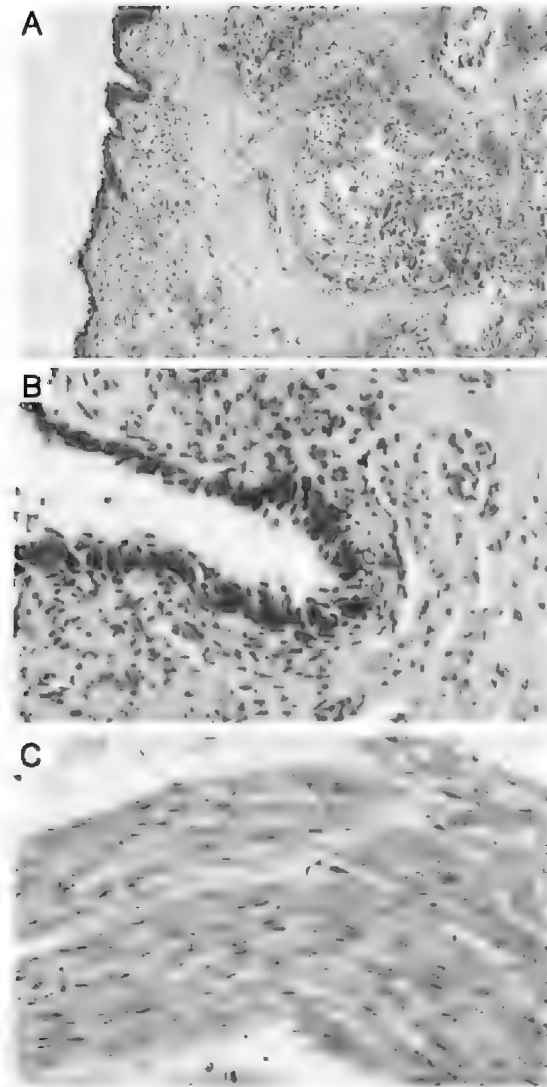


FIG. 3. Histological sections, stained with haematoxylin and eosin, of the ventral diverticulum of QMJM13647. A, low-power view of mucosa and submucosa demonstrating mucous-secreting glands; B, high-power view of mucosa demonstrating non-ciliated, pseudo-stratified epithelium; C, high-power view of stratified muscle typical of voluntary (skeletal) muscle.

## DISCUSSION

Hosokawa (1950) suggested three possible functions for the diverticulum viz. a valve to prevent water and/or food entering the respiratory tract; a reservoir of air to assist respiration while the whale was submerged; a phonation

apparatus. He also noted that its function (if any) may be unrelated to those possibilities. Haldiman & Tarpley (1993) described in detail, by reference to transverse sections, the larynx of an 8.5m long bowhead whale (*Balaena mysticetus*). They considered the diverticulum to be an integral part of the ventral tracheal wall and that its enlargement should act to occlude the tracheal lumen. They also suggested that movement of air, in and out of the diverticulum, could in theory produce sound by 'fluttering' action but noted that the function of the diverticulum is not provable at present. Turner (1872) considered that phonation was possible during expiration by vibration of the elongated caudal processes of the arytenoids and this would not require 'assistance' from the diverticulum. Quayle (1991) suggested that phonation could occur between the opposing arytenoids. Humans who have a supra-cricoid laryngectomy for cancer, in which operation the vocal cords are removed but the arytenoids retained, can produce a satisfactory voice using the arytenoids as the vibratory segment (W.B. Coman, pers. comm.).

I have not examined an adult humpback whale larynx, but Hosokawa (1950) noted that the diverticulum of a humpback whale foetus was small relative to other baleen whales. Baleen whales gulp large volumes of water when feeding and generate high oral and presumably pharyngeal pressures during filtration and deglutition. Consequently, tracheal occlusion may assist in protecting the tracheo-bronchial structures from misplaced water in addition to the usual epiglottic valvular function. There is consensus that the diverticulum of baleen whales is capable of tracheal occlusion. Dissection of an adult humpback whale larynx, particularly a male (the 'singing' sex) in the breeding season when most phonation is believed to occur (Cato, 1991), is awaited to provide a further step in this question which has featured prominently in cetacean scientific literature for two centuries.

## ACKNOWLEDGEMENTS

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**ESTIMATES OF GROUP SIZE AND RATES OF INTERCHANGE BETWEEN HUMPBACK WHALES IN THE WHITSUNDAY ISLANDS AND HERVEY BAY, QUEENSLAND. (ABSTRACT)** From 1993-1999 we spent 719 days in the Whitsunday Islands (298 days) and Hervey Bay, Queensland (421 days) studying humpback whale (*Megaptera novaeangliae*) utilisation patterns of these two important migratory destinations of Group V whales. A total 182 days (1,102 hours) were spent on the water in the Whitsundays, and 239 days (1,964 hours) in Hervey Bay. We photo-identified (on the basis of tail-fluke shots alone) individual whales 1,567 times. Comparison of photographs showed these identifications included 1,212 whales, 315 observed first in the Whitsundays and 897 observed first in Hervey Bay. Of the 1,212 whales identified, 106 were photo-identified in both locations. Sighting data included date, time, GPS location, pod size, age/sex class of identified animal, sea state, and surface water temperature. Sex was

determined for 215 whales (156 females and 59 males) either by genital photo (58 females and 48 males), presence of calf (98 females), or occurrence of singing (11 males). Data have been analysed to provide population estimates for each location and to determine the rate of exchange between the two areas. Photos have also been compared to the overall East Australia Humpback Whale Fluke Catalogue (now at 2,192 individuals). Resight histories and calving rate of identified females have been determined. The migratory characteristics of animals moving between the Whitsunday Islands and Hervey Bay has important implications for the management of whalewatching operations along the Queensland coast.

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**OVERWINTERING NORTH PACIFIC HUMPBACK WHALES IN ALASKAN WATERS. (ABSTRACT)** Humpback whales (*Megaptera novaeangliae*) are present year-round in southeastern Alaska. It has been unknown if the whales observed in midwinter eventually migrate to a mating and calving ground or forgo migration for that year. This study documents true overwintering on a feeding ground, where a whale was sighted often enough to determine that migration could not have occurred that winter.

Sighting histories were compiled for individually identified whales present in southeastern Alaska between mid December and mid April, 1994-2000. These data showed that more than 150 different whales were present at some time during these seven winters. Whales included calves, yearlings, juveniles, adults, males, pregnant females (known by the presence of a calf later that year or the next winter), mothers still with their calves and females recently separated from

their calves. Ten occurrences of overwintering were documented for nine whales; one in 1997, four in 1998, one in 1999 and four in 2000. One whale overwintered twice, in 1998 and 2000. The other whales were not sighted often enough to rule out a late migration from the feeding grounds or an early return from the mating and calving grounds.

The implications of overwintering humpback whales and an extremely staggered migration are significant. These findings could alter traditional methods of estimating key life history parameters because many population assessment models (i.e. population estimates) are dependent upon the assumption that all whales are available for sighting on the mating and calving grounds each winter.

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**ECOLOGICAL RESEARCH AND THE HUMPBACK WHALE IN ANTARCTIC WATERS. (ABSTRACT)** The Southern Ocean Cetacean Ecosystem Program (SOCEP) has been operating in Antarctic waters south of Australia since mid-1995. It aims to address ecological and management questions concerning cetaceans in the Southern Ocean, on a range of ecological scales, using a multispecies, multidisciplinary, collaborative approach. Humpback whales (*Megaptera novaeangliae*) have long been known to occur in patchy aggregations in particular regions of the Antarctic in the austral summer. SOCEP research has attempted to explain humpback and other baleen whale distribution, by relating it to underlying physical and ecological patterns and processes. These are now starting to become apparent. The annual cycle of spread and retreat of sea ice, combined with complex

effects of physical and biological oceanography, result in heterogeneous summer productivity in different parts of the Southern Ocean. Understanding the role of ecosystem processes in humpback whale distribution and movements (within and between seasons and years) will allow us to determine important habitats for this species on their southern feeding grounds. In future this knowledge may help us to assess the effects of environmental changes on the ecosystem in general, and on the whales in particular.

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# MIGRATORY DESTINATION OF HUMPBACK WHALES WINTERING IN MEXICAN PACIFIC.

(ABSTRACT) Migratory destinations of humpback whales (*Megaptera novaeangliae*) that winter off the Pacific coast of Mexico were examined using photo-identification. Fluke photographs taken from the three main whale aggregations in this area: 383 from Mainland coast; 471 from Baja California Peninsula; and 450 from Revillagigedo Archipelago, photographed between 1983 and 1993 were compared with collections from all known feeding grounds in the North Pacific: off California-Oregon-Washington (COW, 593); off British Columbia (BC, 48); off southeastern Alaska (SEA, 429); Prince William Sound (PWS, 141); and from western Gulf of Alaska (WGOA, 133). The migratory movements of these whales were clearly non-random. Results of the photographic comparisons and statistical tests show clear evidence for preferred migratory destinations of humpback whales from Mainland and Baja California to COW and BC feeding regions. Nevertheless, differences in whale abundance estimates indicate the presence of some unsampled feeding region(s). The picture is different for the Revillagigedo region; although we found matches with all the

feeding regions sampled, no principal migratory destination was detected. This supports the assumption that humpback whales from Revillagigedo belong to a stock separate to the 'American' stock. Based on known abundance estimates, historical whaling records and genetic structure of the populations, we propose that these whales could occupy their historical distribution off the Aleutian Islands and/or the Bering Sea and this feeding ground(s) would be the main summer destination of the whales from Revillagigedo and the area were the missing whales from Baja California, Mainland, Japan and Hawaii feed. Our data from different regions of Mexico support the conclusion that a link between the known BC-COW areas and Baja California-Mainland-Central America regions evidences a distinct subpopulation. We also conclude that this coastal subpopulation is relatively distinct from that of Revillagigedo; however the preferred summer destination for this subpopulation is still unknown.

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# GENETIC RELATEDNESS AND POPULATION COMPOSITION IN HUMPBACK WHALES MIGRATING OFF EASTERN AUSTRALIA.

(ABSTRACT) A combination of nuclear and mitochondrial genetic markers were employed to investigate, a) the role of kinship in group formation during the humpback whale (*Megaptera novaeangliae*) migration, and b) the population composition of whales travelling along the eastern Australian migratory corridor.

We analysed 57 pods sampled off eastern Australia throughout the 1992 migration. The sample included 99 males and 43 females (skewed sex-ratio reflecting male predominance in migrating humpback whales). Pod size ranged between 2 and 5 individuals. In 43 (75.4%) pods all members were sampled. All individual whales were screened for 8 nuclear genetic markers (microsatellites). A total of 90 (63.4%) individuals were sequenced for a portion (371bp) of the mitochondrial DNA control region, both to verify kinship identification and to assess the stock composition of the study population.

Individual genetic profiles were compared at three levels, in order to identify: identical genotypes, parent/offspring

pairs and relatedness among individuals (within/between groups, between sexes and between migratory phases). In the attempt to identify eventual kin aggregations among whales migrating in spatial and/or temporal proximity, both pods and 'day-clusters' (whales sampled on the same day) were used in our analyses. Mitochondrial haplotypes were compared with those available from world-wide conspecifics.

Twenty-one pairs of first-degree relatives were found. Apart from females with neonates or yearlings (4), migrating whales of either sex did not seem to select their partners based on kinship at any stage of the migration. Our data suggest that the study animals were representative of a large, panmictic population.

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# MANAGEMENT AND MONITORING OF HERVEY BAY WHALE WATCHING: QUEENSLAND PARKS AND WILDLIFE SERVICE.

(ABSTRACT) The Hervey Bay whale watch industry grew from a small fleet of local vessels operated by commercial fishers who realised the potential of humpback whale (*Megaptera novaeangliae*) watching in the waters of Hervey Bay. As popularity grew the Department of Environment and Conservation realised the need to manage and monitor human activities near humpback whales to ensure their protection. In 1989 the Hervey Bay Marine Park was gazetted and a zoning plan released.

Under Queensland's *Nature Conservation Act 1992*, humpback whales are declared a protected species and scheduled as 'vulnerable'. The *Nature Conservation (Whales and Dolphins) Conservation Plan 1997* was released to protect cetaceans in Queensland waters.

From August 1 to November 30 each year, the Hervey Bay Marine Park is zoned as a Whale Management and Monitoring Area. Today, Queensland Parks and Wildlife

Service (QPWS) are the responsible agency for permitted activities relating to humpback whales. A maximum of twenty commercial whale watch permits are available under the QPWS policy model (which dictates vessel lengths and speeds for commercial whale watching) and the *Nature Conservation (Whales and Dolphins) Conservation Plan 1997* to assist management of tourist programs based on humpback whales, and associated vessel use.

QPWS compliance monitoring includes vessel patrols and covert operations. A *Standard for Whale Watching Educational Programs* has been developed as a tool to ensure commercial whale watch programs provide information to clients of a standard satisfactory to the Chief Executive of QPWS.

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